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Vol. IV

VASCULAR CRYPTOGAMS (PTERIDOPHYTA)

By

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PREFACE TO THE THIRD EDITION

The present edition of the book has been thoroughly revised in order to keep with the recent developments in the subject and many suggestions received from colleagues all over India. Chapters incorporating life cycles of *Isoetes*, *Salvinia* and *Azolla* have been added. A large number of figures have been redrawn and some new diagrams have been added to illustrate some aspects of morphology and development.

Some chapters have been revised to extricate details not required for the degree students. In doing so much care has been taken not to eliminate recent information and to give legitimate details and provide an informative reading to the teachers and inquisitive students.

The author has received many useful suggestions from colleagues all over India. The author wishes to express his thanks and sincerest gratitude separately in the acknowledgement.

It is a sincerest request to my colleagues to point out to we the defects and drawbacks in the present edition so as to enable him to improve the book in the subsequent editions.

PREFACE TO THE FIRST EDITION

The study of vascular cryptogams forms an essential part of our syllabi for both undergraduate and post-graduate students. It is an interesting assemblage of plants that inhabited land for the first time and became established to a terrestrial mode of life. Their

study reveals a striking array of characters that speak of their antiquity is early land plants. This book is designed so as to acquaint the students with the structure and reproduction of these remarkable vascular, but seedless plants.

The book, in its present form is meant for the degree students and covers the syllabi of most of the Indian Universities. It was decided to give a detailed account of the structure and reproduction of the representative types of vascular cryptogams so as to equip the undergraduates with a thorough information about them. Without such an information it is impossible to follow a comparative account and a generalised treatment of the subject at advanced levels. With this idea in mind the author deviated from the trend of giving brief life history descriptions that do not satisfy the inquisitive students. Tremendous amount of research has been carried, during the past twenty-five years or so, on the various aspects of these lowly organised vascular plants and many new and interesting facts have been brought to our knowledge. With the increase in the knowledge of the fossil history of the group some newer interpretations regarding the conquest of land and origin of vascular cryptogams have been advanced. Most of these hypothesis have been dealt with in Chapter One. Lot of experimental work has been done and is being done on the problems of apospory and apogamy. Interesting results have been obtained as a result of studies on tissue culture in India and abroad. A brief discussion on these topics has been included in the first chapter. Such an information is necessary for the students so as to equip them with modern trends in the subject. These valuable informations are given in the research papers that are not easily available to the students. Their brief description in this book will certainly go a long way to enhance the horizon of knowledge of the students in the colleges. Lot of additional information is incorporated in the chapters dealing with the life histories of representative types. This has added to the volume of the chapters concerned. The author has also deviated, at certain places from old text book versions of some topics. This was necessitated on account of some recent work on these topics and newer interpretations. The authority and the year of publication have been quoted in all such cases.

This book is not an outcome of author's original research but is a compilation work incorporating the researches of the pteridologists in India and abroad. The matter has been compiled from standard texts, reviews, monographs and research journals in a manner suitable to the degree students. The language of the book

is simple and easily understandable. It is profusely illustrated. Most of the figures have been redrawn or adapted from standard books, journals, monographs and research papers. Sources of all such figures have been duly acknowledged in their legends. Some figures have been drawn from actual specimens and prepared slides. These were drawn with the help of Camera Lucida or otherwise, by the author himself.

A short bibliography has been given at the end. It includes some of the recent publications, but is in no way a complete and a comprehensive compilation as is not needed for such an elementary type of book. To save space titles of papers have been omitted and only the names of the authors, years of publication and the names of journals have been given.

The author wishes to express his indebtedness to the authors and the publishers of standard texts, monographs, research journals and reviews from where the matter of this book has been compiled. The eminent among the authors who deserve special mention are D. H. Campbell ; F. O. Bower ; D. H. Scott ; C. W. Wardlaw ; Elizabeth, G. Cutter ; I. Manton ; P. N. Mehra ; T. S. Mahabale; H. Y. Mohan Ram ; D. W. Bierhorst ; A. Arber ; H. C. Bold; H. N. Andrews ; G. M. Smith and K. R. Sporne.

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I offer my thanks to my publishers particularly Shri Shyam Lal Gupta and Shri Rajinder Kumar Gupta for bringing out this volume.

It is a sincere request to my colleagues all over India to point out the defects and give useful suggestions to improve the book.

Government College, P. C. VASISHTA
Chandigarh.
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CONTENTS

CHAPTER I

THE VASCULAR CRYPTOGAMS (PTERIDOPHYTA)

lycopsids, sphenopsids and ferns) are treated as vascular crypto-

[illegible]

of spores.

[illegible]

their ancestors. *Psilotum* and *Tmesipteris*, our two surviving remnants of *Psilopsida* retain the primitive features of the first land plants.

In the pages ahead we shall discuss the characteristics of the living Pteridophytes or the seedless vascular cryptogams.

Characteristic Features

(*a*) **Sporophyte.** The vascular cryptogams possess an independent sporophyte with a vascular system. It exhibits a great variation

in form, size and structure. All the living pteridophytes are nearly herbaceous except a few woody tree ferns. [illegible] dorsiventral or radial in [illegible] ly branched [illegible] The roots are [illegible] short lived. [illegible] by means of a single, two-sided [illegible] apical cell or by a plurality of such apical initials. A distinct apical meristem has [illegible] eported in a number of [illegible] sculature of the sporophyte [illegible] protostele (siphonostele), [illegible] polycyclic stelar organisation [illegible] present in some [illegible] is absent [illegible] exception [illegible] **sporous** [illegible] *Isoetes*, [illegible] called the [illegible] by leaf-like appendages called the sporophylls [illegible] the sporophylls may be scattere[illegible] or may be restricted to a particul[illegible] They are in many cases compacted to form distinct spore producing regions called the **cones** or the **strobili** (*Selaginella*, *Equisetum*). The sporangia, in some cases may be produced within specialised structures called the **sporocarps** (*Marsilea*, [illegible] distinct segregation of vegetative and [illegible] have also been reported in some [illegible] *arvense*, *Matteuccia struthiopteris*). [illegible] may be *eusporangiate* or *lepto-sporan*[illegible] and germinate to give rise to the gametophyte [illegible]

(*b*) **Gametophyte**. The homosporous pteridophytes generally have monoecious prothalli. They may be **protandrous** or **protogynous** (*Equisetum*). Dioecious prothalli have also been reported in *Equisetum* and some ferns (*Pteris*, *Pteridium*, [illegible] in homo[illegible] [illegible]

The sex organs may [illegible] the bryophytes in general [illegible] invariably four longitudina[illegible] from two to six cells. The [illegible] and *Equisetum*) to 14 in [illegible] The antheridial [illegible] or *Leptosporangiate*. The [illegible] enclosing a variable number [illegible] stalks or may be sessile. [illegible] number of cells in a jacket also varies from 3—many. The gametophytes are **exosporic** in homosporous forms and **endosporic** in heterosporous forms.

The zygote develops into an embryo within the archegonial [illegible] and is surrounded and nourished by the prothallial tissue.

The development of the embryo may be **endoscopic, exoscopic** or **lateral.** (See chapter VIII for details).

The alternation of generations is **heterologous** in all the vascular cryptogams.

Alternation of generations

Hofmeister (1851) used this term in plants. He observed that in Mosses and Ferns there are two types of morphologically distinct individuals in the life cycle. Both alternate in a life cycle *i.e.*, there are some events which lead one generation to produce the other and thus cause alternation. The actual phenomenon responsible for bringing about alternation was exposed by the significant discovery of "the Periodic Reduction of Chromosomes" by Strasburger (1894). Strasburger discovered the process of **meiosis** in plants. This discovery revealed that the reduction in the number of chromosomes leads to the formation of a new individual in the life cycle. This individual has haploid number of Chromosomes in its nuclei. It bears sex organs and is concerned with sexual reproduction. It was given the name **'gametophyte'** and represented **gametophytic generation.** The haploid gametes unite (**fertilization** or **syngamy**) and establish a diploid nucleus or a **synkaryon.** Fertilization established a diploid cell or the **zygote,** which is a pioneer structure of the diploid individual or the **sporophyte.** It germinates to form the embryo, which in turn develops into the sporophyte individual. This generation is termed the **sporophyte generation** The sporophyte individual bears sporangia which produce spores as a result of **meiosis.** These spores are haploid and are also known as **meiospores.** The spores are the pioneer structures of the gametophyte generation. They germinate to give rise to the gametophyte individual known as the **prothallus** in vascular cryptogams.

Both the generations can reproduce vegetatively and effect an increase in the number of their individuals.

The above events, as displayed by the normal life cycle of a vascular plant, lead us to the following conclusions; (i) There are two distinct individuals in the life cycle of vascular cryptogams (ii) These individuals are produced by the germination of the haploid spores and the diploid zygote. (iii) The one produced by the spores is the **gametophyte** plant. To it is attributed the function of sexual reproduction and is haploid. (iv) The zygote produces the embryo which gives rise to the diploid individual called the **sporophyte.** It bears haploid spores (or meiospores) after a process called **meiosis.** (v) The two generations alternate with each other in the life cycle. (vi) Meiosis and syngamy (fertilization) are the two significant stages that switch on the life cycle from one generation to the other. (vii) The number of chromosomes is halved during meiosis and is doubled during syngamy or fertilisation.

We can reach the same conclusions, as outlined above, if we study the life cycles of the bryophytes. The only difference between

the bryophytes and the vascular plants is that in the former the gametophyte is an independent and a dominant individual, whereas the sporophyte is a reduced and a rather inconspicuous individual dependent wholly or partially on the gametophyte. There is, however, an evidence of progressive elaboration of the sporophyte in the bryophytes, but it never becomes fully independent and is always short-lived as compared to the gametophyte. In the vascular plants the case is reverse. The sporophyte individual is a complicated, independent and a dominant generation, whereas the gametophyte is comparatively much reduced. The gametophyte in the homosporous forms, though inconspicuous and comparatively short-lived, is independent and may be surface living and ... (autophyti... green ... exospc... ...are not enclosed by the spore wall. They are also infected by an endophytic or a mycorhizic fungus in some genera (*Lycopodium*), *Psilotum* and *Tmesipteris*). The hetrosporous land plants, surprisingly enough, display a considerable reduction in their gametophytes. The gametophytes are reduced and **endosporic**. They have, as a rule, separate male and female prothalli. The male prothallus is extremely reduced and represented only by a single prothallial cell. The female prothallus, on the contrary, is well developed because it has to nourish the developing embryo. Such a dioecism is not unknown in homosporous land plants, but is a regular feature in the heterosporous ferns. The life cycles of homosporous and heterosporous vascular plants are represented diagrammatically in Fig. 1.1, A, B.

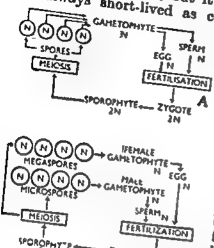

Fig. 1.1. A. Pattern of life cycle in homosporous vascular cryptogams.
B. Life cycle in a heterosporous vascular cryptogam.

The sporophyte in the vascular cryptogams is no doubt independent but it has to depend upon the gametophyte during its earlier stages of development. It achieves its complexity after establishing its independence. The sporophyte, however complex it may be, has never achieved complete independence. The huge and giant sporophytes of the gymnosperms, during their earlier stages of development, are completely at the mercy of the food stored in the gametophyte. This is true even in the case of apogamously formed sporophytes. This food in the homosporous plants is truly gametophytic in origin, but in the heterosporous plants the food is mainly drawn from the sporophyte plant and is only stored in the gametophytic tissue. The angiosperms, on the other extreme, tell a different tale. The food stored in the endosperm is derived from the sporophyte and is stored in a triploid tissue. The morphological complexities of the sporophyte of vascular plants coupled with their elaborate and well ...nised anatomical set-up and equipped with efficient means of

dispersal confer upon them the potentialities to live under vari environmental conditions. These capabilities are responsible f their being stamped as efficient land dwellers.

Both the homosporous and heterosporous vascular plant exhibit **heteromorphic** type of alternation of generations because the sporophyte and the gametophyte individuals present marked morphological and anatomical differences. The same is the case in the bryophytes.

While studying the life cycle of a heterosporous individual a common feature that attracts our attention is the difference in the size of spores. It poses a serious question before us. Why the microspores (smaller in size) give rise to the male gametophyte and the megaspores to the female gametophyte? This question has not been satisfactorily answered. Two possible reasons have no doubt been suggested

The first suggestion tends to explain the cause of difference in size. The megaspores are larger in size and produce female prothalli. The latter have to lodge the developing embryo sporophyte that requires lot of nourishment. The larger spores have greater nutritional store and can produce a well developed female prothallus that is capable of hoarding food sufficient for the development of embryo sporophyte. The microspores are smaller in size and thus have little food stored in their protoplasts. They cannot afford to produce massive prothallial tissues. They germinate to develop one or two-celled prothallus that bears a single antheridium. The function of the antheridium is to produce spermatozoids. After their liberation, it has nothing to do and, therefore, perishes. This can be the cause of their smaller size. The microspores are produced in large numbers as they are likely to be wasted during dissemination.

The cause of their being unisexual appears to be a contrivance towards cross pollination. The monoecious or bisexual gametophytes of homosporous vascular plants have many chances of self-fertilisation, unless they are submerged under water. The dioecious prothalli have extremely rare chances of self-fertilisation and suffer from a great disadvantage if they grow under terrestrial conditions. Under such circumstances they have little chance of fertilisation because the spermatozoids cannot reach the archegonia. This difficulty is solved to a greater extent by the phenomenon of heterospory. The microspores that need not carry much food are light in weight and smaller in size They can be easily carried by wind and other agents to the female prothalli. The chances of their wastage are eliminated to a great extent, on account of their large number per microsporangium. Those which fall on the female prothallus have absolutely no difficulty in effecting fertilisation as the spermatozoids have not to travel a long distance and require only a little moisture which is provided by dew drops. Chances of self-fertilisation under these circumstances are rare, and cross-fertilisation is usually effected. This leads to outbreeding and ultimately to

...ations and rapid evolution. Heterospory has, a matter of fact, ...uatic environments. Such an emanci... has conferred on the sporophyte the freedom to grow under varied environmental conditions. Heterospory is, therefore, regarded as a necessary step towards the evolution of seed habit and must be significant development during the struggle to conquer land.

Sex Expression

... is another very important factor that should not be lost sight of ...ms. *This is* ...ametophyte *difference in* ...ecious pro... evident only not possible ...

... cryptogams can tell that ... spores to the female prothalli, ... plants this property of sex determination has shifted to the sporophytic individual. In ... evident from the position and structure of ...

Origin of Alternation of Generations

Celakovsky (1874) listed three distinct types of alternation of generations in plants. These are :—

... Generations by which he meant the ...

2. The Homologous Alternation of Generations that was believed by him to be prevalent among algae and fungi.

3. Strophogenesis or the alternation of shoots.

... the terms **antithetic** and **homologous** and repla... for antithetic theory and **Transform...** These two theories have been advanced ...f generations. Both of them are aimed ...ic individual in the life cycle.

Interpolation or Antithetic Theory

...was put forth by Bower and later supported by Overton (1893), Scott ... Bower discussed it in ...

was available only ...

(i) Development of jacketed sex organs especially the archegonium.

(ii) The retention of the fertilised egg within the archegonium that could provide it with sufficient food.

(iii) The zygote or the fertilised egg divided mitotically and not meiotically to form a diploid embryo, which in primitive land plants distinguished into a sterile jacket enclosing a number of diploid cells or spore mother cells.

(iv) The diploid spore mother cells underwent meiosis to form tetrads of haploid spores. Such a primitive sporophyte is exemplified by *Riccia*.

(v) Gradually the primitive sporophyte underwent progressive sterilisation and gave rise to complex sporophytes of liverworts like *Marchantia*, *Anthoceros* and *Mosses*. These sporophytes were dependent wholly or partially upon the gametophytes for food.

The events of apogamy and apospory were dismissed by Bower as 'ex post facto' events. He stated, "They illustrate the potentialities of plants of present day rather than evolutionary features of the remote past, and will have no part in producing that normal alternation which is characteristic of the Archegoniatae."

Homologous or Transformation Theory — Pringsheim

This theory was put forth by Pringsheim (1876–77) and has a large

1. Existence of isomorphic alternation of generations in the algae e.g., *Cladophora*, *Ulva*, *Ectocarpus* and *Dictyota*. Both the generations are photosynthetic.

2. Presence of Chloroplasts in the sporophytes of some bryophytes.

3. Presence of tracheids in the gametophytes of some lower cryptogams e.g., *Psilotum*.

4. Occurrence of phenomenon of apospory and apogamy. These deviations from the normal life cycle suggest that either generation can arise ... tic individual ... apospory the ... phenomena ... cation of the

The supporters of this theory further believe that the free living sporophyte later became attached to the gametophyte and partially dependent upon it. Such a step leads to the reduction in complexity of the sporophyte as in the bryophytes. Further reduction leads to the origin of simple and ... This *permanent retention* of the ... be responsible for the develop ... generations and led to the ... *generations in the bryophytes.* ... is retained within the gametophyte.

Modern evidence provides more support for the homologous origin of ... 1960) but even if we accept this theory ... phological differences between the sporo- ... must be certain factors which initiate the ... for the distinct morphological character- ... metophyte. Two hypotheses have been advanced to explain these differences.

A. Lang's Hypothesis

Lang introduced his hypothesis in the year 1909. He emphasized that the spore and the zygote, which are the first cells of the gametophyte and the sporophyte respectively develop under different environmental conditions. The spores after dissemination are free from the influence of the sporophyte and are freely exposed to external environments. The zygote, on the other hand ...

... ating generations may be sufficient to account for the differences between them. This hypothesis has recently been put to experimental tests and some favourable results have been achieved. So far it has not been possible to produce a sporophyte from a spore. Ward and Wetmore (1954) and Jayasekera and Bell (1959) were successful in ... by cutting away archegonial t... embryos of various ages or ... and were successful in germin... from the influence of the gametophyte. In most of these experiments the freed tissue underwent abnormal development, but ultimately was able to produce a sporophyte. It, however, shows that gametophytic influences are significant in the development of the sporophyte, but not necessary. In *Todea barbara* the freed zygotes produced small thalloid structures of gametophytic nature, but it was not possible to achieve the formation of sex organs on these thallus-like structures.

B. Blackman's Hypothesis

Blackman (1909) attached no importance to the different environmental conditions to which the zygote and the spore are prone. He expressed the opinion that differences in the chromosome numbers and other intrinsic differences between spore and the zygote are responsible for morphological differences in the structures produced by their germination. Bell (1963) made cytochemical and ultrastructural studies on the fern egg cell and concluded that there are many cytochemical and cytological differences between the spore and the egg cell.

It appears that the views expressed in both the hypotheses are partially correct. Environmental, cytoplasmic, nutritional and hormonal and genetic factors coupled together appear to be responsible for the distinct developmental differences between the two generations. None of these hypotheses have taken into consideration the effect of organic and inorganic nutrition and of hormones on the developmental pattern of the spore and the zygote. Recent experimental data collected on a number of ferns indicate the importance

of hormonal and nutritional factors in controlling the development of the zygote. Bistow (1962) experimented with the callus tissue derived from the sporophyte of *Pteris cretica*. He found that the callus remained undifferentiated on a medium containing sucrose and high concentration of auxin. In a medium containing sucrose alone the callus developed into a sporophyte. If the callus is grown in a medium containing only mineral nutrients it differentiated into a gametophyte. Whittier (1962) and Whittier and Steeves (1960, 1962) could induce the apogamous production of sporophytes from a number of otherwise normal fern gametophytes by the incorporation of suitable sugar concentrations in the culture medium. Wetmore et al (1963) demonstrated that when prothalli of *Onoclea*, *Osmunda*, and *Todea* are planted erect on a medium containing one per cent sucrose, cylindrical and sturdy growths, containing a vascular strand of xylem elements are produced. De Maggio (1964) was able to induce the formation of sporophytic buds and roots on the prothalli of *Lycopodium obscurum* grown in a culture medium containing coconut milk and sucrose. These experiments reveal the importance of nutritional factors in determining the morphological differences between the two alternating generations of the vascular cryptogams.

Modern Concept.

The studies on tissue culture and the effect of
the development of sporophytic or g...
to postulate two hypothes
lates the presence of a gene ...n be
stimulated into action. T ...ation of various
organs in fern sporophytes ... gene block controlling the
formation of root, leaf or ga...hyte can be stimulated into action in any
cell whether it is of a sporophyte or that of a gametophyte. Every gene
block has a master gene for that block and it is necessary to activate this
master gene in order to trigger into action any subdivision of a gene block;
(ii) The second hypothesis concerns the phenomenon of alternation of generations. These studies lead us to disbelieve the *Antithetic* and *Homologous* theories of alternation of generations; but instead confirm our belief in a third theory called the Genetic Theory of alternation of generations. This theory postulates that a change in the genetic system in the early progenitors of land plants brought into being two distinct and independent individuals in the life cycle of the land plants. These individuals may be identical or dissimilar in appearance.

Abnormalities in the Life Cycle

The normal life cycle of a vascular plant has two alternating generations. These are the diploid sporophyte and the haploid gametophyte. Both alternate regularly in the life cycle and this alternation is brought about by two significant steps known as the **fertilisation** and the **meiosis**. The regular alternation of chromosome numbers is sometimes impaired by the occurence of two common phenomena known as **apogamy** and **apospory**. They will be dealt with separately.

Apogamy : It was first reported by Farlow (1874) in *Pteris cretica*. Apogamy can be defined as the development of a sporophyte directly from the gametophyte without the intervention of sex organs and gametes. The sporophytes thus formed usually have the same chromosome number as the gametophyte i.e., haploid number for the species. Apogamy occurs in nature and has also been induced under experimental conditions. It is a common and a widespread phenomenon in the ferns. Natural apogamy has been reported in more than 50 species of ferns belonging to 20 genera. In

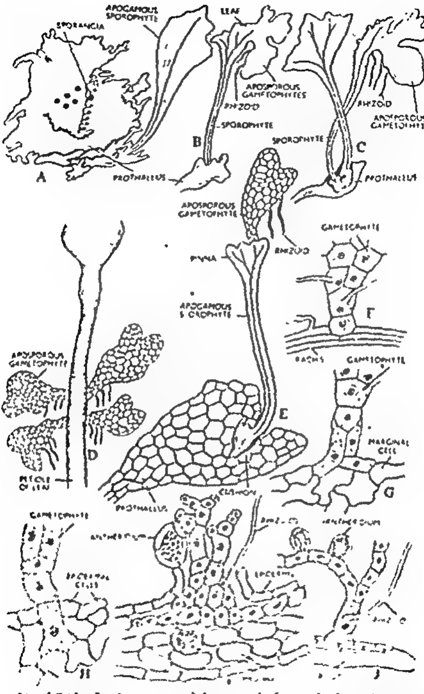

Fig. 1.2 (A–J). Apogamy and Apospory in ferns. A. Apogamous sporophyte arising from the gametophyte of *Phyllitis scolopendrium* (After Lang); B–C. Aposporous gametophytes arising from the primary leaves of sporophyte of *Osmunda regalis* (After Lang); D. Aposporous gametophytes arising from the petiole of *Pteris* [illegible] (After [illegible]); E. Apogamously produced [illegible] of *P.* [illegible] bearing aposporous gametophyte (After [illegible]); F–J. Aposporous gametophytes of [illegible]; F. Prothallus arising from epidermal cell of rachis; G. Prothallus arising from marginal cells of a pinna; H. [illegible]

some species of ferns apogamy appears to be a necessity and is a regular process. It is perhaps due to the inherited constitution of the plant. Natural apogamy is commonly known in *Dryopteris*, *Pteris*, *Pellaea*, *Adiantum*, *Osmunda*, *Todea*, *Athyrium*, *Cheilanthes*, *Polystichum*, *Asplenium*, etc. To this list can be added a number of genera and species in which apogamy has been experimentally induced. Cases of parthenogenetic development of the egg into the sporophyte are not included under apogamy, because it is the development of vegetative tissue of the prothallus into the sporophyte. Apart from the ferns apogamy has also been induced in some species of *Lycopodium*, and *Equisetum*

Causes of Apogamy

Regarding the causes of apogamy, several explanations have been put forth. Lang (1898) induced the formation of sporophytic buds (Fig. 1·2 A), roots, sporangia (Fig. 1·3) and tracheids in various fern prothalli by avoiding watering of the prothalli from above. Brown (1923) summarised literature regarding the induction of apogamy by avoiding fertilisation of the egg. Many workers regard failure of normal fertilisation as a cause of apogamous production of sporophytes. Mottier (1931), however, demonstrated that in *Matteuccia struthiopteris* failure of fertilisation does not induce apogamy. Brown (1923) induced apogamy in *Phegopteris polypodioides* by avoiding normal fertilisation. Other conditions favouring apogamy have also been suggested. These are: culture in bright light and at higher temperatures (Nathansohn, 1900); by lowering the vitality of the prothallus by fungal and algal attack; and failure of formation of functional sex organs under various unfavourable nutritional conditions. Williams (1938) suggested that in addition to the environmental factors there must also be some internal factors such as the nature of inherent susceptibility due to abnormal nuclear composition and behaviour, that bring about apogamy.

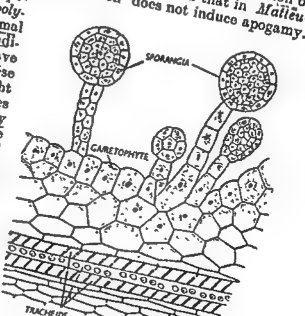

Fig. 1·3. Apogamy in *Phyllitis scolopendrium*. Note the sporangia have developed from the prothallial tissue that has also developed tracheids (After Lang).

Ageing of the prothallus has also been regarded as one of the factors influencing apogamous developments on the prothalli of some ferns. Recent work (Whittier and Steeves, 1960) in *Osmunda*, *Adiantum* and *Pteridium* has shown that apogamy can

be induced by growing the prothalli on an agar culture medium rich in glucose. Wetmore and his associates (1963) demonstrated that when prothalli of *Onoclea*, *Osmunda* and *Todea* are planted erect on a medium containing one per cent sucrose, cylindrical and radially symmetrical growths with vascular strands are produced. De Maggio (1964) induced the formation of sporophytic buds on the prothalli of *Lycopodium obscurum* grown in culture media containing coconut milk and sucrose. These experiments reveal the effect of nutritional factors in inducing apogamy. Loyal and Chopra (1973) induced apogamy in *Regnellidium diphyllum*.

Cytology of Apogamy. Work during the last 15 or 20 years has revealed that one out of every 15 species of ferns has what

n generations have

w arises as to how

tologically. Two

which is rare, both

the processes of spore formation and fertilisation are eliminated from the life cycle. The sporophyte or the fern plant produces a prothallus or the gametophyte which arises as a bud from the leaf and develops into a full-fledged prothallus. It is produced from the

diploid tissue

This diploid

rise to sporop

a method, t

apogamy in the same plant. It is not a common method and has since been reported in *Athyrium filix foemina* var. *clarissima*, *Dryopteris filix-mass* var. *cristata apospora* (Farmer and Digby, 1907); and in *Trichomanes kraussiana* (Georgevitch, 1910). Sarbadhikari (1939) discovered it in *Osmunda javanica*. It has been induced in *Pteris vittata* by Palta.

phyte is 60 the spore mother cells in such ferns will have 120 chromosomes. They will

and is by far the co

Aspidium falcatum; by Steil (1919) in *Nephrodium hirteps*; by Dopp (1932-1933) in *Aspidium filix-mas* var. *cristata*, and *Dryopteris*

remotium; by Patternson (1942) in *Polystichum tsussemense*; by Mehra (1944) in *Adiantum lunulatum*; and by Mehra and his students (see Mehra, 1961) in thirty species of Himalayan ferns (*Pteris cretica*, *P. aspercaulis*, *P. blumeana*, *P. biaurita*; *Dryopteris paleacea*, *D. fibrillosa*, *D. odontoloma*, *D. atrata*; *Adiantum caudatum* and others). Mehra (1961) has given a vivid description of the apogamous and aposporous Himalayan ferns and has discussed their bearing on speciation and phyletic relationship among the ferns. On the basis of his intensive research on the cytogenetical constitution of apogamous ferns in the Himalayan region and his knowledge about the work done elsewhere he grouped them into five categories. These are: (i) **Diploid apomicts** which are of two types and include the species *Dryopteris paleacea*, *Pteris cretica*, *Adiantum lunulatum* and *Drypopteris borreri* (ii) **Tr**[illegible]**ploid apomicts** that are of [illegible] [illegible]pecies; (iii) **tetrap**[illegible] [illegible]nd include about [illegible] only three species [illegible] *Adiantum hispidul*[illegible] [illegible] comprehensive analysis is not w[illegible] scope of this book.

Recently Evans (1965) has reported an interesting case of apogamy in a species of *Polypodium*. In this case he reported the formation of 32 mitospores in the sporangia. The sporangia have 16 spore mother cells which do not undergo meiosis, but instead divide mitotically into 32 spores. These spores are reniform in shape and occur in diads rather than tetrads. He reported this sequence to occur regularly in all sporangia. The spor[illegible] readily to form prothalli which bear [illegible] buds. The prothalli bear stomata but produc[illegible] species on which Evans worked was a triplo[illegible] [illegible] supposed parents were tetraploids. It is an example of genetically fixed taxon that is barred from interaction with other taxa. Heun (1939) reported the absence of reduction division in the spore mother cells in *Pteris cretica* var. *albo-lineata*. He reported that spore mother cells form tetrads of [illegible] and there is no meiosis. [illegible] shows the formation of [illegible] M. Marzenti (1967) repo[illegible] [illegible] and *A. plenum*. In both the species the s[illegible] [illegible] cells do not undergo reduction division and act directly as spores. These spores germinate to produce gametophytes that bear antheridia containing viable sperms, and also bear apogamus sporophytes.

A very interesting fern gametophyte was discovered by a bryologist A. J. Sharp from the Appalachian region of North America. He [illegible] place it among the bryophytes. This game[illegible] they are only rudimentary. It [illegible] and is a ribbon like and branchin[illegible] of marginal clusters of cells or [illegible] [illegible] sporophytes under natural cond[illegible] *Vittaria* (shoe string fern) [illegible] tion. It is considered [illegible] Stokey (1951) cultured [illegible] [illegible] was able to induce the formation of small [illegible] sporophytes directly from the gametophyte. These apogamously produced sporophytes had certain diagnostic features of the Vittariaceae.

Investigations on the [illegible] enable[illegible]

Apospory. The phenomenon of apospory was recorded by Druery (1884) in a fern called *Athyrium filix-femina* var. *clarissima.*

apospory sp
ment of gam
without the
of *Trichomai*
produced from soral regions of the leaf and from leaf tips. Later apospory was reported by Farlow (1889) in *Pteridium aquilinum*, by Goebel (1905) in *Asplenium dimorphum*, by Kupper (1906) in *Asplenium dimorphum*, by Lang (1924) in *Osmunda regalis* (Fig 1·2, B,C), by Lawton (1932, 1936) in 13 species of ferns, by Beyerle (1932) in 34 ferns and by Sarbadhikari (1936) in *Osmunda javanica*. Druery and Neurnberg (1938) and Steil (1939, 1951) reviewed the literature on apospory and apogamy in ferns. Steil (1944) was able to induce apospory in *Tectaria trifoliata.* Bristow (1962) developed gametophytes from a callus tissue derive
Pteris cretica. This callus devel
in media containing only mineral
(1961) isolated zygotes and unc
able to induce
that resem-
d many cases
of apospory in ferns and was tempted to state that the phenomenon of apospory must be general among ferns. Wetmore and De Maggio (1963) have also reviewed cases of apospory and apogamy among ferns.

Cytology and Artificial Induction of Apospory

reported the forma-
f the young or old
f as heart-shaped
prothalli bore an-
roduce archegonia.
these aposporously
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The game-
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n induced
may lead
to the formation of octaploid sporophytes. Lawton also observed where the diploid gametes of diploid aposporous gametophytes

cross fertilise with haploid gametophyte and produce triploid sporophytes. Lawton (1932) also induced apospory in *Aspidium marginale* and *Woodwardia virginica* and produced tetraploid sporophytes. Manton (1932) induced apospory in *Osmunda regalis* and produced diploid, triploid and tetraploid gametophytes and sporophytes.

W. N. Steil (1944) induced the formation of aposporous gametophytes on the young leaves of apogamously produced sporophytes of *Tectaria trifoliata*. He was able to induce the formation of gametophytes from the margins of the young leaves and from the hair borne on the petiole of the first formed leaf of the sporophyte. In both the cases the gametophytes were produced in large numbers.

Goebel (1907) and Palta (unpublished) induced the formation of prothalli from the petiole and laminar surfaces of the pinnae in *Pteris vittata* (Fig 1·2, D). Goebel also observed the formation of thalloid structures bearing antheridia, rhizoids, stomata, and even vascular strands on the detached juvenile leaves of *Alsophila van-geertii* and *Ceratopteris thalictroides*. These thalloid structures resembled gametophytes in possessing antheridia and rhizoids and sporophytes in possessing stomata and vascular strands. He designated them as "Mittelbildungen". Development of tracheids and stomata are no longer regarded as indicative of aposporous or apogamous developments, but are considered to have developed under the influence of chemical environments under which the organs are cultured. So formation of stomata and tracheids do not give these aposporously developed gametophytes the characteristics of sporophytes. They can be regarded as purely gametophytic structures because they bear antheridia and rhizoids.

Beyerle (1932) observed the formation of undifferentiated outgrowths on the isolated leaves of some ferns. He observed them to grow into prothalli in *Aneimia densa*, *Pteris tremula*, *Anogramma leptophylla*, *Polypodium heracleum*, *Cibotium schiedei* (leaf margin), *Dicksonia fibrosa* (leaf margin), and *Drynaria heraclea* (small and dying leaves).

Woronin (1908) reported the development of aposporous gametophytes on the attached primary leaves of *Pellaea nivea*. Koehler (1920) induced the formation of prothalli on the leaves of *Platycerium bifurcatum* grown in dim light. Under strong light the leaves produced shoot buds.

Brown (1918) reported an interesting case of regeneration from the petioles of the leaves of *Phegopteris polypodioides*. Under experimental conditions a cellular mass of green cells developed on the cultured petioles. It grew into a prothallus that bore rhizoids, true leaves, and structures intermediate between leaves and prothallia. It is a queer case of development of sporophytic and gametophytic structures together. Such instances clearly indicate that there is no inherent difference between the two alternating generations (sporophyte and gametophyte), and consequently no clear relation to chromosome number.

Charles Morlang (1967) induced apospory in three species of *Asplenium* (*A. platyneuron*, *A rhizophyllum* and *A. montanum*). He cultured the leaves cut from the sexually produced sporophytes of these ferns, under controlled conditions. The leaves were observed to produce two types of neoplastic growths. These were two dimensional growths and three dimensional growths. The former developed into a normal heart-shaped prothallus that produced both types of sex organs that bore gametes. They had a diploid chromosome complement. The three dimensional growths developed into sporophytes.

... n *Pteridium* ... growth of ... margins of ... n mesophyll ...

Causes of Apospory

Several factors seem to influence the aposporous development of gametophytes from vegetative tissues of the sporophyte :—

... mineral nutrition is ... allus tissue obtained ... ie ...

2. Goebel (1902) and Beyerle (1932) demonstrated that there is a pronounced relation between the stage of development of sporophytic cells (under culture) and the kind of organs regenerated. They observed that in *Ceratopteris thalictroides* aposporous gametophyte developed on decapitated young sporophytes with one or two leaves whereas in older sporophytes only shoot buds developed. Beyerle (1932) observed that in *Davallia canariensis* and in *Nephrolepis biserrata* the prothalli develop on leaf tips and shoot buds at the basal and older parts of the leaf.

3. In some ferns e g., *Drync* ... and *P. heracleum* the leaves devel ... sporophytic buds under strong li ... trated that in *Platycerium bifurcatum* prothalli develop on leaves grown under dim light whereas the same leaves produce sporophytic buds on exposure to strong light.

4. The work done in Panjab University Botany Laboratories (Mehra and Palta, 1969 unpublished) on tissue culture has revealed interesting results that have far-reaching conclusions. A few examples are being cited here They obtained root callus tissue from the roots of a tetraploid *Cyclosorus dentatus* on Knudson's medium +2% sucrose+2, 4—D. The callus was fragile and its cell suspensions were obtained in sterile distilled water. The isolated cells of the callus were then placed on three different media :

A. Knudson's medium basal.

B. Knudson's medium+1% sucrose.

C. Knudson's medium+2% sucrose.

In A the root cells behaved as spores and germinated, to give rise to a prothallus. This shows that under mineral nutrition the callus tissue is induced to form gametophytes because basal Knudson's medium contains only minerals. In B the callus cells gave rise to structures that were partly gametophytes and partly sporophytes. They called such structures as Gameto-sporophytes. In C the callus cells gave rise to the complete sporophyte (regeneration).

Apospory has also been induced in *Pteris vittata* by Palta (unpublished). Sexually produced normal sporophytes produced gametophytes from the juvenile leaves. These gametophytes bore normal sex organs in Knudson's medium without sucrose. In this very species he was able to produce apogamous sporophytes on KM with 2% sucrose. Later this apogamous sporophyte was placed in KM without sucrose. After 3 weeks time the apical pinnae of the same sporophyte produced aposporous gametophytes (Fig. 1·2, E). So with a change in the nutritional set-up of the environments apogamy and apospory can be induced at any time.

Aposporous gametophytes have also been induced on scales, roots and juvenile leaves in *Cyclosorus dentatus*.

Resemblances with Bryophytes and Gymnosperms :—

The pteridophytes resemble the bryophytes in the following respects :—

hetero

1. Both have heterologous alternation of generations.
2. Both have multicellular and jacketed sex organs. The male sex organs are called the *antheridia* and the female *archegonia*.
3. Both have a distinct embryo stage after fertilization.
4. Asexual reproduction by mitospores is absent in both.
5. Both have motile male gametes and non-motile female gametes. The female gametes are retained within the venters of the archegonia.
6. In both sexual reproduction is oogamous.
7. In some pteridophytes, *e.g.*, *Psilotum* roots are lacking and rhizoids are the only source of anchorage and absorption.
8. In both the gametophytes are independent, except in the heterosporous pteridophytes like *Selaginella*.
9. Both have homosporous sporophytes (there are exceptions in the pteeridophytes).
10. Water is essential for fertilization in both groups.

The pteridophytes resemble the gymnosperms in the following respects :—

1. Both have independent and well-developed sporophytes that are distinguished into root stem and leaves.
2. In both the sporophytes have a distinct vascular system. *Heterosporous pteridophytes* have *inconspicuous* gametophytes that are wholly or partially dependent upon the sporophyte.
3. The xylem lacks vessels in majority of pteridophytes and gymnosperms.
4. The phloem lacks companion-cells.
5. Sexual reproduction is oogamous. In some gymnosperms, *e.g.*, cycadales the sperms are motile like the pteridophytes. Heterospory is prevalant in some pteridophytes.
6. Asexual reproduction by mitospores is absent.
7. There is a distinct embryo stage.
8. Alternations of generations is heterologous.
9. There is a great resemblance between the foliage of cycads and tree ferns.

Origin of the Vascular Cryptogams

A number of theories have been put forward to explain the origin of the vascular cryptogams. All of them tend to explain the origin of the independent sporophyte and are based on two assumptions :

1. [illegible] originated from an anthocerotean type of a bryophyte.

2. The adherents of the second view believe algae to be the ancestors [illegible] The proponents of this idea trace the origin of [illegible]

Anthocerotean Theory

It was put forth by Campbell (1859) and later supported by Smith (1938). Presence of intercalary meristem and photosynthetic tissue in the sporophyte of *Anthoceros* lead Campbell (1895, 1899) to put forth the view that such sporophytes are very near to the independent sporophytes of the vascular [illegible] the foot of the sporophytes in *Anthoceros* [illegible]

(*i*) The intercalary meristem of Anthoceros-like sporophytes shifted to he apex and initiated dichotomous branching (Fig. 1.4, A—D).

(ii) Dichotomous branching (Fig. 1-4) necessitated the formation of terminal sporangia like those of the Psilophytales (*Rhynia*, and *Psilophyton*).

(iii) Metamorphosis of the anthocerotean columella into a conductive strand.

(iv) Occurrence of conducting tissue in the lower portions of the sporophyte of *Anthoceros fusiformis* (Campbell, 1924) and restriction of spore formation to apical regions alone.

[illegible]

the archegonia of *Anthoceros* and the pteridophytes is the presence of a jacket layer around venter of the former and its absence in the latter. This is due to the divisions of the archegonial initial of *Anthoceros* into three jacket initials and an axial cell. In pteridophytes this division is absent and the initial functions directly as an axial cell. According to Smith obliteration of these divisions of the archegonial initials would lead to the pteridophytean archegonium, which is homologous [illegible] the cover cells and axial row of cells of the anthocerotean [illegible] lia, Smith pointed out that the entire [illegible] lent to the fertile region of the antheri- [illegible]

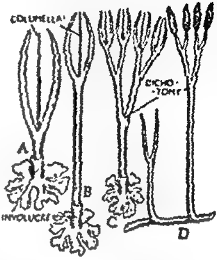

Fig. 1-4. (A—D). A scheme illustrating origin of early land plants from *Anthoceros-like* ancestors (After Smith).

Campbell (1939) compared the simple gametophytes of *Anthoceros* with the green algae. Smith also pointed towards some superficial resemblances between the embryos of *Psilotum* and *Tmesipteris* with those of *Anthoceros*.

This theory has not received wide acclaim and has almost been discarded by the modern botanists.

The Strobilus Theory

It was put forth by Bower in 1894 and supported the origin of sporophytes of vascular cryptogams from the liverworts. According to this theory the simple sporophyte of the liverworts evolved into an elaborate and a complex structure along the following lines :—

1. There was progressive sterilisation of the sporogenous tissue in the live-wort sporophyte. It led to the formation of alternating sterile and fertile regions.

2. The fertile regions or sporangia became superficial in position.

3. The sterile parts gave rise to lateral projections called the **enations**. The enations were either below the sporangia or besides them. At this stage the entire sporophyte looked like a strobilus. The sporangia lie in the axils or at the bases of the enations. Such a condition was visualised in *Phylloglossum*, *Isoetes* and those species of *Lycopodium* where all the leaves are sporophylls.

4. Ultimately the sporangia shifted on to the enations. The enations could then be called the **sporangiophores** or the **sporophylls**.

5. Further sterilisation led to the disappearance of sporangia on the

sporophylls. This step led to the formation of sterile lateral appendages called the leaves.

6. The *central columella-like part increased considerably* in size and became an axis or the stem bearing leaves and sporophylls.

7. The leaves and sporophylls later became large and elaborate.

8. The roots *developed* from the base of the stem and stamped the sporophyte as an independent plant.

... ...rded and has only historical importance. ... as belonging to the psilophytales does ... ple sporophyte as pictured by Bower. ... branched *stems* that were not small. ... it explains the origin of ... that the microphylls which ... in his strobilus ... Later, Bower, ... plain only the ... leading to the ... Zimmermann's ...

Protocorm Theory

This theory was put forth by Treub in 1884. He regarded the proto... embryos as a *primitive organ* and *considered it to be* ... d in some contemporary species ... sted that it *might* have been *of* ... vascular cryptogams. This idea ... orphologists *and is now of histori*... garded the protocorm as "oppor... re. He attached only ecological ... in establishing the young sporo... ...ocorm as a modi... ...

Phyton Theory

This theory was put forward by Celakovsky in 1901. He denied the existence of the stem as an independent member. *His theory* was closely ... *strobilus theory* of Bowver because he postulated that the early ... was nothing but a *cluster of* leaves or ... n the sporophyll bases. Schoute (1931) ... *severely criticised* Celakovsky's *memoir* ... structed a *scheme of thought without* ... his ideas, which can be explained otherwise also.

... and Gaudichaud (1841) were the earlier authors who gave ... morphologists. Wolff made a very frank ... e plant except the *leaves* and stem. *He* ... of the stem. The stem was regarded to be ... stalks. His views were later elaborated by ... (1901).

Algal Origin of the Vascular Cryptogams

The consensus of opinion now favours the view that early land plants originated from an algal ancestor. The algal origin of the vascular Cryptogams and the seed plants is supported by the following facts :

1. The chloroplasts of both the green algae and the vascular cryptogams *contain chlorophyll a and b.*

2. Most of the carotenoid pigments in these groups are also similar.

3. Their carbohydrate reserves are similar. Their starch grains contain a mixture of two types of glucose macromolecules, amylose and amylopectin.

4. Their cell wall structure and composition are also similar, e.g. the cells in both the groups are characteristically surrounded by a pectic wall layer that contains galacturonic acid and a wall layer containing cellulose.

5. The flagella in the male gametes of vascular cryptogams like those of green algae are of whip-lash type.

Lotsy (1909) traced the origin of vascular plants from a chaetophoraceous green alga. Fritsch (1945) suggested that such an alga must have been an erect and parenchymatous form with isomorphic alternation of generations. All these authors believed that bryophyta and the vascular cryptogams are two parallel lines of evolution and that there is no phylogenetic connection between them. Gregus (1955), Andrews (1956), Leclercq (1951), Axelrod

1. **Church's Hypothesis.**—Dr. Church in his publication entitled "Thalassiophyta and the sub-aerial Transmigration" conjectured a polyphyletic origin for the vascular land plants. He wrote his essay without any

the sea bottom started rising at certain places and the plankton stage was succeeded by the 'Benthic Stage,' which included a number of attached and rooted sea weeds. This process went on for ages and the attached sea weeds gradually attained a very high degree of organisation. This uplift of sea bottom was accompanied by a large number of environmental changes that included increase in the amount of atmospheric oxygen and light intensity. The uprising sea bottom later emerged out of the sea and that was the first sight of land. This brought in the conditions of desiccation and insolation. The sea weeds which emerged out of water along with the land were now under terrestrial environments and were exposed to free oxygen, light and desiccation. This led to struggle for existence among the exposed algae and brought in adaptations among them. Natural selection played its role and more adapted changes accompanied by variations were brought about in these sea weeds. Church believed that land plants originated under tropical con-

to take on a new function of absorption. The spores needed a resistant cell wall to equip them for the changes and chances of dissemination by air. Accord-

ing to Church the sporangial tetrads of the early vascular plants originated from the unilocular tetrasporangia of the algal ancestors. The female sex

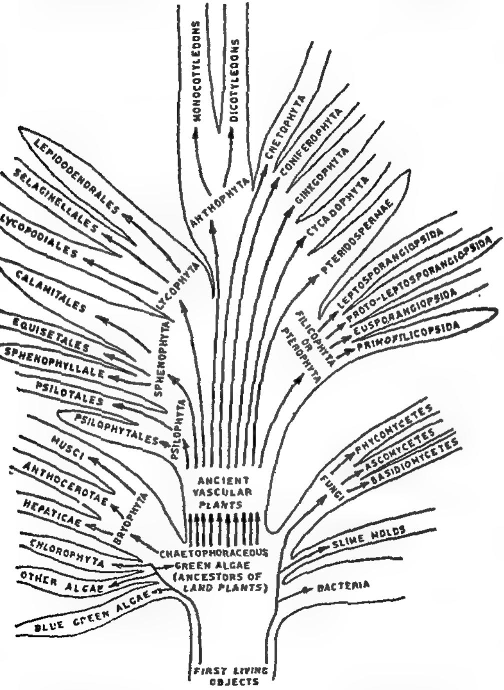

Fig. 1·5. Schematic representation of the phylogenetic relationships among plants and polyphyletic origin of vascular plants (Based on Axelrod).

organs or the archegonia were postulated to have evolved independently along lines. Both the gametophytes and the sporophytes were believed to

be already leafy and autophytic. It appears from the above description that brown algae were considered to be the probable ancestors of the land plants.

The geologists do not regard the land to have emerged from the sea. They believe that land was already in existence when the oceans appeared. Church's hypothesis, therefore, is not considered to be tenable. Moreover it has been urged that the highly organised transmigrant brown algae that were used to marine environment were too specialised to adapt entirely to new mode of existence on dry land.

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D.H. Scott (1924) while upholding Church's view stated, "The chief fact on which we have to rely is that some of the early Devonian land plants, though vascular, are much like sea weeds in their external characters. The Rhynie discoveries so far as they go, tend to support, in a general way, the view that the vascular plants came from fairly high algae."

2. **Greguss's Hypothesis.** Greguss put forth his views in 1955. He traced the origin of vascular plants from the three major divisions of algae, *i.e.*, Chlorophyta, Phaeophyta and Rhodophyta. He did not take into consideration the pigment constitution, the products of photosynthesis, and the presence or absence of cilia in the reproductive units. He laid stress on the branching of the organisms *i.e.*, whether it is dichotomous, monopodial or verticillate. He derived mosses from Chlorophyceae and liverworts from the Phaeophyceae. In the same way he traced the origin of the *Rhynia* and *Hornеophyton* from the Chlorophyceae and *Psilotum* and *Tmesipteris* from the Phaeophyceae. His hypothesis is quite untenable and is not based on sound knowledge of the various living and extinct groups of the vascular plants. Lam (1957) criticised Greguss's hypothesis and regarded it as based on unsound footings. He almost disregarded the phylogenetic relationship of the plant groups while tracing their orgin *e.g.*, Psilophytales and Psilotales that are quite closely related to each other have been regarded as descendants of two different algal groups.

3. **Andrews' Hypothesis.** *Andrews* (1956, 1959) also believed in the polyphyletic origin of vascular plants. His conclusions are based on the discovery of some peculiar fossils that are not vascular plants but can be regarded as descendants of marine algae that made several attempts to conquer land. These are [illegible]

[illegible]

belief was strengthened due to diversity in the morphology and structure of the various groups of land plants such as Lycophyta, Psilophyta, Articulatae (Sphenophyta) and Pterophyta. He considered that morphological and structural variations presented by these main divisions of vascular cryptogams are due to their origin along various and independent lines of evolution from different algae rather than from 3 or 4 groups. He gave a vivid description of the important fossils from the early Palaeozoic in 1959 and then commented on Zimmermann's telome concept. He supported his concept regarding the evolution of the pteropsids and sphenopsids, but disregarded his concept for the evolution of the lycopsids and dismissed it as a purely hypothetic approach.

4. Leclercq's Hypothesis. [illegible]

ancestral algal complex. As a result of her palaeopalynological studies of the early land plants that inhabited the earth from the Upper Devonian down to the Cambrian, she concluded that the land plants originated in the pre-Cambrian period. Her studies on the form and structure of the spores in correlation between these ores from lower horizons d that land plants existed ted in the Pre-Cambrian period. She also reviewed the extinct land plants belonging to the Middle Devonian, upper Silurian and Cambrian periods. She found that the Rhyne fossils (*Rhynia*, *Horneophyton*) that were discovered by Kidston and Lang were of quite simple organisation as compared to those which occurred in earlier periods like the Upper Silurian. The fossils belonging to this period were quite complex and elaborate and, therefore, led her to conclude that simple psilophytes like *Rhynia* and *Horneophyton* are not primitive and ancestral, but represent the last remnants of a dying race that might have flourished in the earlier ages (Pre-Ordovician). She concluded that the psilophytes like *Rhynia* and *Horneophyton* are the last and recent in the series that had an independent origin from the algal stock.

5. Axelrod's Hypothesis. Axelrod (1959) followed the lines of Leclerct and Andrews and regarded the vascular cryptogams to have originated along different phyletic lines of evolution from diverse algal stocks (Fig. 1·5). He regarded *Rhynia* and its allies as 'bradyletic types' and not ancestral to the other Pteridophytes. Discovery of sixty different types of spores with cutinised and resistant walls from the Cambrian period led him to believe that land plants originated somewhere far down in the pre-Cambrian age from diverse algal stocks. The idea is based on the assumption that these spore types belonged to the early land plants that might have colonised the land in the Cambrian period. The transmigrants evolved from these algal stocks were

originating from the pre-Cambrian algal stock. These five lines represent the five hypothetical transmigrants from where the five major divisions of ... These are the ... leading ... erophyta ... s or the ... lso arose ... ta. The ... Anthophyta. Axelrod's phyletic scheme regarded ... lophyta, Lepidophyta, Filicophyta, Arthrophyta) and the Pteridospermophyta to have originated independently and directly from the independent algal stocks (Fig. 1·5).

6. Merker's Hypothesis. Merker (1961) postulated that the land plants along with the Bryophytes originated independently from a group of pre-Cambrian archegoniates which in turn were derived from different algal sources. He recongnised the following five evolutionary off-shoots from the ancestral archegoniates :—

1. Extinct Rhyniaceae, Psilotales and Ophioglossaceae.
2. Bryopsida which include the liverworts and mosses.
3. The Sphenopsida.
4. The Lycopsida.
5. The Pteropsida and Pteridosperms, Gymnosperms and Angiosperms were believed to have evolved from the Pteridosperms.

Merker considered that the gametophytes and the sporophytes in the ancestral archegoniates were almost alike and independent. Such a condition persisted in the first evolutionary line of origin, which included Rhyniaceae,

P. N. Mehra.

quest on Land & Evolutionary pattern in Early land plants

Psilotales and Ophioglossaceae. During the course of evolution the sporophytes either progressed or regressed. The former lines are represented by Lycopsids, Sphenopsids and Pteropsids. The latter line is represented by the Bryopsida. He regarded Rhyniaceae as reduced and simplified forms and not a primitive and ancestral group of land plants.

Mehra (1968) raised an objection against the ... of ... of ... at it is not possible to believe in their independent origin along various lines from the algal ancestors. The antheridium is also of the same embedded type in the primitive vascular cryp- ...

7. Lam's Hypothesis. Lam (1955) suggested a diphyletic origin for ...

There are two well founded objections to this hypothesis (Mehra, 1968). To derive coniferopsida from the Lycopsid stock does not appear to be justified. The second objection is that Lam grouped *Casuarina* with other members of the Gnetophyta. *Casuarina* is very much an Angiosperm and should not have been grouped with the Gnetophyta. It is, however, known from biochemical analysis (Alston and Turner, 1966) that *Casuarina* is a unique angiosperm that produces compounds called biflavonyls. These compounds are not produced by any other angiosperm, but are produced by many Cycads, conifers and other gymnosperms. In its lignin chemistry also *Casuarina* resembles gymnosperms. These chemical features which are unique for this genus cannot be ignored in determing its phyletic relations.

8. Mehra's Hyphothesis Professor P. N. Mehra in his fifteenth Albert Charles Seward Memorial Lecture entitled "Conquest of Land and Evolutionary patterns in Early land plants" gave a vivid description of the evolutionary patterns in the early land plants and summarised the views regarding the origin of land plants. While concluding his lecture he proposed his own hypothesis (Fig. 1-6) explaining the origin of land plants (1968).

He postulated that the green algae (Chlorophyta) ...

... around the sex organs. Development of these structures enabled these transmigrating plants to desiccation. These plants were erect, non-vascular, had similar ... and gametophytes (Isomorphic alternation) that were ... and photosynthetic, both had apical cell organisation and were constructed. Such a group of plants could live under subaerial ... Mehra called them Protoarchegoniatae (Fig 1-6). From these ,

goniatae there diverged two lines of evolution : (A) the psilophytaceous line of evolution : and (B) the Lycopodiaceous line of evolution.

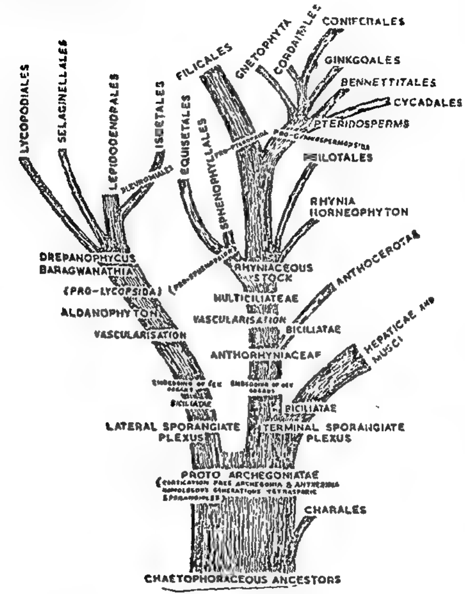


Fig. 1·6. Mehra's scheme of polyphyletic origin of vascular plants (After P.N. Mehra).

(A) Psilophytaceous Line of Evolution. The Protoarchegoniate ... possessed jacketed sex organs ... with apical cell segmentation ... ns were projecting type, super- ... ndependent and their terminal ... re terminal and had a distinct ... rise to a terminal sporangiate ... a the archegonia after fertiliza- ... orophytes of this plexus follow-

(a) Along one line the sporophytes, developing from the oospores en- ... remained attached to ... gametophyte. The ... rses of development. ... d, whereas along the ... phytes with the for- ... the mosses, where- ... Both the lines of evolution ended blindly. The spermatozoids were biciliate.

(b) This line of evolution led to the appearance of vascular tissues in the sporophytes which remained independent and became well established ... mbedded sex organs with multifla- ... , however, bore terminal sporangia ... This led to the appearance of the ... out into the following four lines of evolution :

(i) **Prosphenopsid line.** It was linked with the Rhyniaceous stock by plants like *Protohyenia*, which gave rise to *Hyenia* and *Calamophyton* of the early and middle Devonian periods. From them arose the sphenophyta (Equisetales).

(ii) **Pro-pteropsid line.** It was linked with the Rhyniaceous stock through *Protopteridum* like plants. They had terminal sporangia but also bore short sterile branches with **Circinate ptyxis.** Such plants gave rise to the Filicales or Filicophyta.

(iii) **Progymnospermopsid line.** It is represented by *Archaeopteris*, *Callixylon* type of plants that showed secondary growth. Some of them had also established heterospory. They gave rise to the pteridosperms on one hand and to Gnetophyta, Cordaitales, Coniferales and Ginkogoales along other independent lines of evolution. The pteridosperms gave rise to the Bennettitales and the Cycadales.

(iv) **Psilophytaceous line.** It bifurcated into two lines of evolution. One culminated in Rhyniaceae whereas the other gave rise to the Psilotales represented in the modern flora by *Psilotum* and *Tmesipteris*.

(B) **Lycopodiaceous Line of Evolution.** It started directly from the ... lateral ... denarales and Isoetales through Pleuromiales.

Professor Mehra has not indicated the origin of angiosperms in his scheme. The problem of origin of angiosperms is still an abominable mystery.

Majority of the botanists ...

EVOLUTION OF THE SPOROPHYTE

According to a general belief the earliest and the ... sporophyte of the land plants was axial in nature. ... leaves

branches were evolved later by a modification of the central stem. These primitive land plants were supposed to have rootless, leafless and dichotomously branched green stems. The vascular system was a simple protostele. Some of the ultimate branches terminated in sporangia This assumption is supported by the discovery of some simple plants in the upper Silurian and Devonian periods of earth's history (*Rhynia*, *Horneophyton*, *Psilophyton*, *Asteroxylon* and others). Discovery of such plants led many botanists to propose theories explaining the appearance of leaves, branches, roots and sporangia on the sporophyte. These theories tend to explain the process of elaboration of the primitive sporophyte into the modern sporophyte possessing roots, leaves and variously disposed sporangia. Of all these theories **Telome theory** of Zimmermann (1930) has atracted great attention and has a large number of supporters.

Telome Theory - Zimmermann → origin from –

This theory was first proposed by Zimmermann in 1930 and later elaborated by him in 1938 (Manual of Pteridology, 558-618). Zimmermann postulated that all the vascular plants evolved from a very simple, leafless and a dichotomously branched ancestral type like *Rhynia*. Such a plant is made up of sterile and fertile branches. T [illegible] The simple and termina [illegible] ted as telomes [illegible] point of fork [illegible] **mesomes** (Fig. 1·7). The telomes were classified as sterile or vegetative telomes also called **phylloids** and **fertile telomes**. The fertile telome consists of a terminal and a stalked sporangium usually [illegible] to its base. As evolution [illegible] ran- [illegible] the telome trusses [illegible] syntelomes [illegible] were [illegible] sporangial trusses [illegible] telome trusses were called [illegible] phylloid trusses. [illegible] types of **syntelomes** also [illegible] mixed telome **trusses** or **mixed syntelomes.**

Zimmermann postulated that the primitive vascular cryptogams originated from the green algae. The unicellular green algae divided in all planes to form a parenchymatous thallus. Later **meristematic** tissues developed and erect radially constructed branches came into existence. It was followed by the appearence of distinct alternating generations. The sporophyte branched dichotomously and possessed a central conducting strand. Such algal ancestors, according to Zimmermann, led to the evolution of early vascular plants of the upper Silurian and Devonian periods. They possessed *heteromorphic alternation of generations* and their sporophytes were simple and dichotomously branched. Some of the branches terminated in sporangia They possessed no leaves and had no roots. The vascular system was a simple protostele. The aerial and simple stems possessed stomata. The function of roots performed by hair or rhizoids. These sporophytes had subter-

ranean portions called the rhizomes. All these hypothetical steps are diagrammatically represented in Fig 1.7

These early land plants evolved into the higher vascular cryptogams along three independent lines of evolution. These were the Lycopsid, Sphenopsid and Pteropsid trends of evolution. During the course of this evolution certain **elementary processes** of progressive differentiation took place in the sporophytes. These can be listed as :— (*i*) Overtopping, (*ii*) Planation, (*iii*) Webbing or syngenesis, (*iv*) reduction, and (*v*) recurvation. All these elementary processes of organogenesis were believed to have occurred in varying degress in the different taxonomic groups. These will be discussed separately.

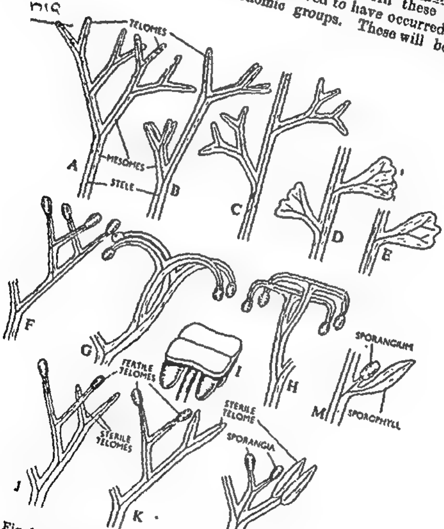


Fig. 1.7 (A—L). Telome concept of Zimmermann.
A. Illustrates hypothesis of telomes and mesomes. B. Overtopping; C. Planation; D—E. Webbing and syngenesis; F-I. Illustrate the origin of the sporangiophores of Sphenophyta by recurvation and fusion and flattening of the telomes and mesomes; J—M. Illustrating the origin of Lycophyta.

Overtopping: The equally dichotomising axes developed unequal dichotomy (Fig. 1.7, B). This resulted in the formation of short and long branches. The short branches appeared as lateral shoots. This led to the development of a sympodial axis which ultimately changed to a monopodial axis with lateral branches These lateral branches metamorphosed into leaves.

Planation: The equal dichotomies were originally in more than one plane. They were arranged in planes successively at right angles (Fig. 1·7 C). During the process of **planation** the dichotomies became arranged in a single plane. It is an important process that led to the evolution of the leaf.

Syngenesis or Webbing: (Fig. 1.7, D—E). As the name indicates the adjacent telomes and mesomes were connected with each other by the development of a parenchymatous tissue between them. This is also called parenchymatous webbing. During this process the *steles of the concerned telomes also fused. Syngenesis was considered* to be of two types by Zimmermann :—

(*a*) **Foliar syngenesis.** During this process there is coalescence or fusion of apical meristems of the telomes. When these meristems fuse to form a marginal meristem, a lamina with veins develops. The activity of these meristems leads to the formation of parenchymatous webs between the telomes. Such developments resulted in the formation of lateral foliar appendages. In case foliar syngenesis is accompanied by overtopping the leaves with pinnate venation are formed. Sometimes foliar syngenesis is accompanie by fusion of the vascular strands. This results in the development of **netveined** leaves or leaves with reticulate venation. Overtopping, planation and foliar webbing brought about the evolution of a megaphyllous leaf.

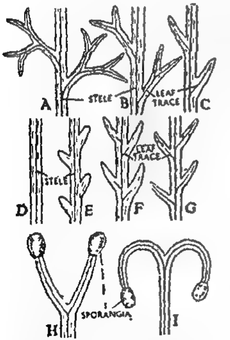


Fig 1.8 (A—I.) A—C. Illustrating reduction of syntelomes to single needle-like lateral appendages (C). D—G. Illustrating origin of microphylls H—I. Recurvation (All after Zimmermann, 1938).

(*b*) **Axial syngenesis.** Zimmermann visualised that during this process there was absorption of a number of branches into a single stout axis. The fusing branches had **protosteles** and their fusion led to the appearance of a complex stelar organisation. In case the shoots united by the formation of parenchymatous webs the resulting stelar was a polystelic condition. In case during axial syn- the steles anastomosed in different manners the resultant

stelar organisation was of diverse types, *e.g.*, siphonostele, eustele, solenostele.

Reduction. It is supposed to have brought about the evolution of simple and unbranched microphyllous leaves of the lycopods (*Lycopodium, Selaginella, Isoetes*). It was brought about by the reduction of (Fig. 1·8, A—C) the syntelome to a single needle-like lateral appendage.

Recurving. During this process the fertile telomes were supposed to become reflexed (Fig. 1·8, H, I). As a result the sporangium assumes an inverted position. Zimmermann called this process as **incurvation.** Wilson (1953) recognised two processes—

(*a*) **Recurvation.** During this process the sporangia bent downwards as in sphenophyta.

(*b*) **Incurvation.** This led to the shifting of the sporangia to the ventral surfaces of the foliar appendages thus bringing about a condition found in the ferns.

Wardlaw (1952), however, pointed out that all these changes can be embraced within one term, which he calls as **recurvation.**

While discussing the above listed five elementary processes of organogenesis as postulated by Zimmermann, it becomes evident that microphyllous leaves originated as a result of the process of **reduction.** The megaphyllous leaves of ferns (Filicophyta) originated as a result of combined processes of overtopping, planation and foliar syngenesis. We shall now discuss the origin of the fertile leaves or the sporophylls as visualised by Zimmermann.

Origin of Sporophylls. The origin of sporophylls in the three main divisions of the vascular cryptogams has been visualised differently by Zimmermann.

Sphenophyta or Arthrophyta. Recurvation and syngenesis were supposed to be the elementary processes that led to the origin of the sporangiophores in the members of this division (Fig. 1·7, F—I). Recurvation led to the downward bending of the sporangia. It was followed by fusion and flattening of the telomes and mesomes to form a peltate disc. Intermediate stages leading to this condition existed in the fossil members of this division, *e.g.*, *Calamophyton, Hyenia, Eviostachya* and *Protocalamostachys*. Planation followed by reduction, however, led to the development of the sterile leaves of this division. The intermediate stages are met with in the fossil genera *Calamopyton* and *Asterocalamites*. The Telome theory gives a satisfactory explanation of the evolution of sporangiophores and sterile leaves in the Sporophyte.

Lycophyta. The sporangia are usually borne in the axils of microphylls in the lycophyta. Such a position was derived by Zimmermann along following steps :

(*i*) There was aggregation of fertile and sterile telomes (Fig. 1·7 J).

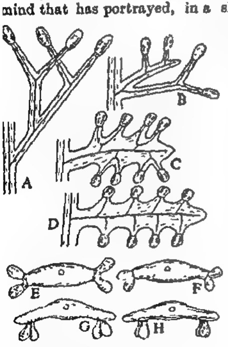
(*ii*) There was reduction in the number of mesomes and the sporangia (Fig 1·7, L, M.) This led to the development of a single leaf with a single sporangium in its axil.

The bifid tips of the sporophylls and leaves of the extinct genus *Protolepidodendron* may be cited as an example of an intermediate type.

Filicophyta or Pterophyta. The elementary processes of overtopping, reduction and folior syngenesis lead to the development of the megaphyllous sporophylls of the ferns. As a result of overtopping, planation and syngenesis a pinnate sporophyll was evolved. The sporangia were marginal in position (Fig. 1·9, C, D). Later recurvation led to the shifting of the sporangia from the margins to the ventral side (Fig. 1·9, F—H). Intermediate types were provided by the extinct genera *Pseudosporochnus*, *Stauropteris*, and *Botryopteris*.

Zimmermann postulated that roots developed from the creeping rhizomes of the primitive or ancestoral types before the evolution of the leaves.

Merits of the Telome Theory. It is an outcome of a master mind that has portrayed, in a skilful manner the origin and evolution of the sporophytes of land plants. Zimmermann has based his theory mostly on account of his comparative study of the fossil as well as living genera of the vascular plants. Many of his assumptions are correct and based on exact phyletic relationships between the various groups of plants both living and extinct. His five 'elementary processes' of planation overtopping, syngenesis, reduction and recurvation give us a unified concept of the manner in which evolution might have proceeded



phyta originated.
A, B. Planation and overtopping; C, D. Syngenesis; E—H. Stages leading to the shifting of sporangia to margin and then to the ventral side of the sporophylls. (After Zimmermann).

an aerial part

The appendages of shoot that is the sporophylls, sporangia and sterile leaves are nothing but modified parts of the stem. While building up his theory Zimmermann has taken into consideration the morphological aspects of the various groups of extinct and living groups of plants.

Demerits of the Telome Theory. This theory is open to criticism in *its* application to the origin of Lycophyta (Lycopsida). The origin of microphyllous leaves of the Lycophyta by reduction of telome trusses is not exemplified by any living or extinct vascular plant. Andrews (1960) has expressed his views on the Telome theory in the following words "Zimmermann's scheme for the pteropsids or at least some pteropsids, has much supporting evidence; his concept for the articulates may be valid, but we are only on the verge of understanding the origin of this group; his concept for the lycopsids is, so far as I am aware, purely hypothetical.".

Enation Theory of Bower. Bower (1935) postulated a theory explaining the origin of microphyllous leaves (Fig. 1·8, D–G). According to enation theory the microphyllous originated as superficial outgrowth from the stem. These outgrowths were originally not supplied by any vascular strand. Later these outgrowths or enations increased in size, the vascular strand reached up to their bases only. Later the leaf trace entered the enations or the lateral outgrowths and traversed its whole length. This vascular supply in the form of a single unbranched strand enervating the individual outgrowth gave them the characteristics of the microphyllous leaves. According to this theory microphylls originated by a process of progressive elaboration and not by reduction as visualised by Zimmermann. *Psilophyton* is an extinct vascular cryptogam belonging to the order. Psilophylates represents the first stage in the process. Another extict member of the same order called *Asteroxylon* represents the next stage where the leaf trace reaches the base of the lateral appendage. In *Drepanophycus*, another extinct member, the leaf trace enters the lateral appendage. Bower's theory is, therefore, to some extent supported by fossil evidence.

Fossil Record and Geological Time Scale

The remains of plants and animals, which lived in the remote past, in many cases, are preserved in the rocks in one form or the other. These are called the **fossils** A brief knowledge of the different types of fossils is essential to know the type of plants that lived in ages bygone and to form an idea of evolutionary process that has gone on for times immemorial and is still going on. A fossil in reality is a clear manifestation of the existence of prehistoric living beings. There are variety of forms of fossils depending upon the conditions under which fossilisation occurred. Common type of fossils are :

1. **Dead and Preserved Bodies.** The actual dead and preserved bodies, or parts of bodies, of plants and animals, with the original tissue intact, and enclosed either in ice or in amber or else mummified in various ways, form this class of fossils

2. **Petrified Fossils.** In these fossils, organic matt been replaced particle for particle, by mineral matter in such

that finer structure of the tissue has been very nicely duplicated and rendered permanent. These types of fossils are numerous and important.

3. **Casts or Molds.** A plant or an animal that has lain in mud or clay long enough to have left its impression; the mud hardens about the bo[illegible] integrates and the m[illegible] the matrix may then [illegible]

4. **Imprints.** These are formed from the burial of plant parts in soils, which harden into rock. The imprint of the organism is left in the rock, after its decomposition. Prints preserve the external features only

5. **Actual Remains.** Such plant fossils are of comparatively young age and do not decompose completely due to low temperature or vacuum. All materials that are resistant to natural decomposition are preserved like this, *e.g.*, cuticle, cutin, sporopollinin in the walls of pollen grains and spores.

6. **Chemical Remains.** Chemical materials like amino acids and hydrocarbons may be obtained in a natural state or in a modified form from the rocks in which organic matter of the petrified plant part or organ has been incorporated.

7. **Products of Activity of Organism.** Some times products excreted by living organism are obtained from the excavations, *e.g.*, secreted lime deposits of algae Such products have been found on pottery and other manufactured goods discovered during excavations.

Geologic Time Scale. With the help of new tools and [illegible] fairly an accurate [illegible] various rock strata, [illegible] salt in the sea and of decomposition of radio-active substances such as uramium and thorium.

On the basis of their st[illegible] logical history of earth into 4 [illegible] and modifications, see Kulp, J. [illegible] these in turn are sub-divided into periods; each period has been split into still smaller units of time intervals called the epochs (see table).

TABLE 1

Geological Time Scale *(Modified after Kulp and Eicher)*

Era	Period	Epoch	Important Plant Events	Beginning in Millions of Years
COENOZOIC	Quarternary	*Pleistocene*	Speciation of herbaceous plants	One
	Tertiary	*Pliocene*	Spread of herbaceous dicots	Thirteen
		Miocene	Rise of herbaceous angiosperms	Twenty-five
		Oligocene	Dispersal of woody angiosperms	Thirty-six
		Eocene	Rise of woody angiosperms now extinct	Fifty-eight
		Paleocene	Modernization of angiosperms	Sixty-three
MESOZOIC	Cretaceous		Earliest known Pines	Hundred thirty five
	Jurassic		Origin of Angiosperms	Hundred and eighty
	Triasic		Spread of Conifers. Rise of Cycads	Two hundred and thirty
PALEOZOIC	Permian		Rise of conifers; coal swamp extinct	Two hundred eighty
	Pennsylvanian	Carboniferous	Widespread coal swamps, formation of coal beds	Three hundred ten
	Mississipian	Carboniferous	Development of coal swamps with gynosperms, lycopsids, sphenopsids and ferns	Three hundred and forty-five
	Devonian		Flourishing psilopsids, lycopsids, sphenopsids, ferns, seed plants and bryophytes. Evidence of brown algae and dinoflagellates	Four hundred five
	Silurian		Cooksonia, the oldest known vascular plant. Record of some non-vascular land plants.	Four hunderd twenty-five
	Ordovician		Marine red and green algae	Five hundred
	Cambrian		Evidence of lime secreting algae.	Six hundred

PRECAMBRIAN	**Late Precambrian**	Eukaryotic organisms	Twelve hundred
	Middle Precambrian	Stromatolites of algal origin. Blue green algae, Bacteria, origin of eukaryotic cell	Two thousand Five hundred
	Early Precambrian	Bacteria like cells and unicellular alga like organisms of age 3,000 million years	Four Thousand Five hundred
		Graphites of possible organic origin	Five thousand
		Origin of procaryotic cell, origin of earth	

Coal Formation

Coal is one of the major fuels in daily [illegible] form of veg[illegible] movements [illegible] remarkable c[illegible] changed them into thick carbonaceous seams which we mine or sometimes quarry in the form of coal. The thickness of the coal seams vary from exposure to exposure.

Geologically speaking, the coal deposits of the world are divisible into two groups as follows :

(1) Carboniferous coal, *i.e.*, coal of carboniferous period of Palaeozoic era, produced about 220 to 275 million years ago.

(2). Tertiary coal : It is comparatively quite younger, produced in nature nearly 70 million years ago.

Based upon the percentage of carbon contents, coal has been classified into four parts as below :

(1) Peat Coal.
(2) Lignite coal.
(3) Bituminous coal.
(4) Anthracite coal.

Anthracite coal is the most pure variety whereas Peat coal is poorest so far as the percentage of carbon contents are concerned.

The Tertiary coal of India is generally of Anthracite quality. The mass with 100% carbon contents is known as diamond which is the hardest known mineral for the present.

India is sufficiently rich in coa ldeposits and it is distributed in almost all the states of the country. The presently known coal deposits of India point to the fact that the country can depend upon coal energy for at least one hundred years more.

CLASSIFICATION

The classification of the vascular cryptogams has undergone vast changes in the recent past. On the basis of the presence or absence of seeds the older taxonomists place the vascular plants

in two divisions: **Pteridophyta** and **Spermatophyta.** The former includes the *primitive vascular plants which bear no seeds.* According to this traditional system of classification the Pteridophytes are divided into the following classes and important orders :—

DIVISION **Pteridophyta**

1. **Class Psilophytineae.**
   (i) Order **Psilotales.** Examples *Psilotum* and *Tmesipteris.*
   (ii) **Psilophytales.** Example *Rhynia.*
2. **Class Lycopodineae.**
   (i) Order **Lycopodiales.** Examples *Ly podium, Selaginella.*
   (ii) Order **Isoetales.** Example *Isoetes.*
   (iii) Order **Lepidodendrales.** Example *Lepidodendron.*
3. **Class Equisetineae.**
   (i) Order **Equisetales** represented by *Equisetum.*
   (ii) Order **Sphenophyllales** represented by *Sphenophyllum.*
4. **Class Filicineae.** It includes the following important orders :
   (i) Order **Filicales.** Examples *Dryopteris, Marsilea,* etc.
   (ii) Order **Marattiales** represented by *Marattia.*
   (iii) Order **Ophioglossales** represented by *Ophioglossum* and *Botrychium.*
   (iv) Order **Osmundales** represented by *Osmunda.*
   (v) **Fossil orders.**

Later some fern-like seed-bearing fossil plants (Cycadofilicales) were discovered. This discovery eliminated the distinction between the two divisions—**Pteridophyta** and **Spermatophyta.** So in the revised systems of classification proposed by Tippo (1942) all the vascular plants are placed in a single division **Tracheophyta.** It is segregated into four taxas which are **Psilopsida, Lycopsida, Sphenopsida** and **Pteropsida.** As to the ranks of these groups, the botanists differ. Some consider them as classes of the division Tracheophyta. Tippo assigns them the ranks of sub-phylla of the phylum Tracheophyta. The terms phylum and sub-phyllum being not in accord with the International Code of Nomenclature, Wardlaw (1955) suggested the rank of sub-divisions for the four groups. The outline of this revised system of classification is given below :

DIVISION **Tracheophyta**

1. **Sub-division Psilopsida**
   . **Class Psilophytineae**
   (i) Order **Psilotales**
   (ii) Order **Psilophytales**
2. **Sub-division Lycopsida**
   Class Lycopodineae
   (i) Order **Lepidodendrales**
   (ii) Order **Lycopodiales.**
   (iii) Order **Pleuromeiales.**
   (iv) Order **Isoetales.**

3. Sub-division **Sphenopsida.**

Class **Equisetineae.**

(i) Order **Equisetales.**
(ii) Order **Sphenophyllales.**
(iii) **Fossil orders.**

4. Sub-division **Pteropsida.** The term is used here in a restrictive sense to cover the megaphyllous pteridophytes only.

Class **Filicineae.**

(i) Order **Ophioglossales.**
(ii) Order **Filicales.**
(iii) Order **Osmundales.**
(iv) Order **Marattiales.**
(v) ***Fossil orders.***

The increasing knowledge about the vascular anatomy and the position of sporangia in the above mentioned sub-divisions has revealed marked divergence among them from one another. The modern writers thus consider that the *differences* between the Psilopsida, Lycopsida, Sphenopsida and Pteropsida series are of the magnitude of a division. Smith (1955), Bold (1957), Benson (1957) and Zimmermann (1939) have given these groups the rank of a division. According to the recommendations of I.C.B.N. (1952) the name of the division should end in the suffix **phyta**, of a sub-division in **phytina** and of a class in **opsida.** On this basis Smith divides the vascular Cryptogams into 4 divisions, **Psilophyta, Lepidophyta, Calamophyta** and **Pterophyta.** Some writers suggest other names. Given below with slight modifications is one of the widely accepted modern classifications of the vascular Cryptogams :—

I. Division Psilophyta. In it are included the most primitive and oldest known land inhabiting vascular plants which are rootless. The sporophyte is differentiated into an underground stem (rhizome), bearing rhizoid-like structures and an aerial shoot system. The leaves when present are small, simple and veinless. There are no leaf-gaps and the vascular cylinder is **protostelic.** The sporangia are *always terminal in position* and *borne singly.* All the members are **homosporous.** The division comprises the following classes :—

1. Class **Psilophytopsida.**

(i) Order **Psilophytales.** *It includes the most primitive fossil* vascular cryptogams with the aerial portion radial and dichotomously branched. Examples are *Rhynia, Horneophyton, etc.*

2. Class **Psilotopsida.**

(i) Order **Psilotales.** It includes two living genera which are allied to the psilophytales. These are *Psilotum* and *Tmesipteris.*

II. Division Lycophyta or **Lepidophyta.** The sporophyte is differentiated into stem, roots and leaves. The leaves are small, with a single vein. The vascular cylinder may be proto-

siphono—or polystelic. The leaf gaps are absent. The sporangia are borne singly either at the base on the adaxial face of the fertile leaf or in its axil. The sporophylls in many Lepidophytes are organized into cones. Some are **homosporous** and others **heterosporous.** On the basis of the presence or absence of ligules, this division may be divided into the following two classes :—

1. Class **Eligulopsida.**

(*i*) Order. **Lycopodiales** The order includes **homosporous, non-ligulate,** forms such as *Lycopodium* and *Phylloglossum.*

2. Class **Ligulopsida.** The class includes **heterosporous** forms with **ligulate** leaves. The four orders recognisable in this class are :—

(*ii*) Order **Selaginellales** represented by *Selaginella.*

(*iii*) Order **Isoetales** represented by *Isoetes.*

(*iv*) Order **Pleuromeiales.** Examples *Pleuromeia.*

(*v*) Order **Lepidodendrales** represented by *Lepidodendron, Stigmaria, Lepidocarpon.*

III. Division Arthrophyta or **Calamophyta** or **Sphenophyta.** The sporophyte is differentiated into stem, roots and leaves. The stems are jointed and marked by longitudinal ridges and grooves. The small, simple leaves are borne in whorls at the nodes. The vascular cylinder may be protostelic or siphonostelic. The leaf gaps are absent. The sporangia bearing organs are specialised appendages called the **sporangiophores.** The sporangiophores are organised into cone-like structures at the terminus of the stem. The division includes two classes :—

1. Class **Sphenophyllopsida.** The class includes the well-known extinct genus *Sphenophyllum* which is placed in the following order :—

(*i*) Order **Sphenophyllales.**

2. Class **Calamopsida.** This class includes both fossil and living forms. The living genus *Equisetum* is referred to the following order:—

(*i*) Order **Equisetales.**

IV. Division Filicophyta or **Pterophyta.** The sporophyte is differentiated into stem, roots and leaves. The leaves are large and usually divided. With the exception of a few protostelic species, the leaf gaps are invariably present. The vascular cylinder is variable. It may be protostelic, siphonostelic, solenostelic or dictyostelic. The sporangia are borne in large numbers either upon the margin or abaxial face of the leaf lamina. With the exception of a few all are **homosporous.** The classes included in this division are given below with the important orders :—

1. Class **Eusporangiopsida.** The sporangium grows from a group of sporangial initials. The wall of the sporangium is more than one cell layer thick. The antheridia are embedded in the prothallus tissue. The class includes the following two orders :—

(*i*) Order **Ophioglossales.** The sporangia are borne on the spike arising from the adaxial face of lamina near its juncture with the petiole.

The order is represented by two important genera—*Ophioglossum* and *Botrychium*.

(ii) Order **Marattiales.** The sporangia are borne on the abaxial face of the leaf blade and are grouped in **sori**. It includes **six** genera of which *Marattia* is well-known.

2. Class **Protoleptosporangiopsida.** The members of this class form a link between Eusporangiopsida and Leptosporangiopsida. The class includes the following order :

(i) Order **Osmundales.** It is represented by three living genera of which *Osmunda* is widely distributed.

3. Class **Leptosporangiopsida.** The sporangium arises from the single sporangial initial. The wall of the sporangium is one cell layer thick. The antheridia are emergent. The modern Pterologists divide the class into the following three orders :

(i) Order **Filicales.** Almost all the members of this order are **homosporous.** The green, thallus-like prothallus bears sex organs on the lower surface. The sporangia are borne in groups called the **sori** on the margin or abaxial face of the sporophyll.

(ii) Order **Marsileales.** It includes **heterosporous** forms. The sori are contained in a special structure called the **sporocarp.** Each sorus contains both microsporangia as well as megasporangia. It includes three genera of which *Marsilea* is the best known.

(iii) Order **Salviniales.** This order includes the heterosporous, free-fl[illegible]ating aquatic forms. The sporangia are produced within the sporocarp, b[illegible]t the latter contains either a single megasporangium or many microsporangia only. The order includes two living genera, *Salvinia* and *Azolla*.

4. Cl[illegible] includes the many extinct [illegible] and (ii) **Coeno**-[illegible]rns and appeared [illegible]alaeozoic.

This system has been followed in this text.

Bold used the term Microphyllophyta instead of Lycophyta. The Microphyllophyta includes all the Lycopods because of their microphyllous leaves. Benson (1957) used the term Pteridophyta instead of Pterophyta. Zimmermann added the Division Noeggerathiophyta.

Doyle (1971, p. 5) divided Pteridophyta into four classes :—

1. Class **Psilopsida** (Psilopsids)
2. Class **Lycopsida** (Lycopsids)
3. Class **Sphenopsida** (Horsetails)
4. Class **Pteropsida** (ferns)

He included these classes under sub-division **Embryophytina** and division **Chlorophyta** (green plants). The seed plants were included under class **Spermopsida.**

Bierhorst (1971) followed the following system of classification :—

Division :—*Tracheophyta*

Class :—*Rhyniopsida.*

Order :—*Rhyniales*

Class :—*Zosterophyllopsida*

Order :—*Zosterophyllales*

Class :—*Lycopodiopsida*

Orders :—*Asteroxylales, Lycopodiales, Protolepidodendrales, Selaginellales, Lepidodendrales, Isoetales.*

Class :—*Cladoxylopsida*
Order :—*Cladoxylales*

Class :—*Equisetopsida*
Orders :—*Hyeniales, Pseudoborniales, Sphenophyllales, Equisetales.*

Class :—*Coenopteridopsida*
Order :—*Coenopteridales*

Class :—*Filicopsida*
Orders :—*Noegerathiales, Filicales, Marsileales, Salviniales*

Class :—*Ophioglossopsida*
Order :—*Ophioglossales*

Class :—*Marattiopsida*
Order :—*Marattiales*

CHAPTER II

PSILOPHYTA

The division Psilophyta includes living as well as extinct representatives. The division shares most of its characteristics with the Psilophytales (discussed below). They have a simple vasculature with xylem lacking vessels and fibres. The tracheids may be spiral, annular, scalariform or even pitted. There is no secondary growth. Mycorrhizal infections are common in the rhizomes (*Psilotum*).

It is divided into two classes:

(*i*) **Class Psilophytopsida.** It includes all the extinct members of this division. It is further divided into a single order Psilophytales which is further split up into families.

(*ii*) **Class Psilotopsida.** It includes the order **Psilotales** which is represented by two living genera *Psilotum* and *Tmesipteris*.

PSILOPHYTOPSIDA

Order **Psilophytales.** They are the simplest extinct vascular plants that were discovered among the rocks of the Early Devonian period of the Palaeozoic age. Among these plants, the first to be recorded (1858) was Sir William Dawson's *Psilophyton princeps* that was discovered from the Gaspe Sandstone. Later it was also recorded in beds of various Devonian horizons in many countries, such as the United States, Scotland, Norway and Belgium. It is the first plant with which our knowledge of the group **Psilophytales** started.

The group Psilophytales was actually recognised and named when the Rhynie discoveries came into light. Our present accurate knowledge of these simple vascular plants is mostly due to investigations of the Rhynie chert-bed. This locality is in Aberdeenshire, and the bed was discovered by the geologist Dr. Mackie in 1913. The plants have been thoroughly worked out by Dr. Kidston and Prof. Lang, whose results are recorded in their remarkable series of memoirs that were published in 1917 to 1921.

The Psilophytales are most prevalent in the lower and the middle Devonian period. They have been recorded by some in the

upper Devonian rocks but the discoveries are not entirely free from doubt. They are characterised by :—1. A simple plant body distinguished into a rhizome and an aerial region. 2. Absence of roots. 3. Rhizoids arise in tufts from rhizome and fix it. 4. The stems branch dichotomously and are naked or covered with small spinous out-growth or reduced leaves. 5. Vasculature is a protostele. 6. Sporangia are terminal and may occur solitary or in groups or in simple racemes. They are not associated with any kind of sporophylls. They appear as swollen stem tips and have a single spore cavity. 7. The wall of the sporangium is several cell layers in thickness. 8. They are homosporous, spores arranged in tetrads. The characteristics are shared by majority of Psilophytales, but variations are there.

CLASSIFICATON

Krausel and Hirmer have put forth a scheme of classification of the group. They divide it into 9 families including more than 20 genera. Out of these 9 families five are most firmly established.

1. **Rhyniaceae.** The plants are rootless and leafless with dichotomously branched aerial shoots. Sporangia are terminal. It includes *Rhynia, Horneophyton, Sporogonites, Cooksonia, Yarravia and Hicklingia.*

2. **Zosterophyllaceae.** The rhizome is profusely branched. Aerial shoots are devoid of leaves. Sporangia are borne on the apices of lateral branches. It includes *Zosterophyllum* and *Bucheria.*

3. **Psilophytaceae.** Plant body as in Rhyniaceae. The aerial shoots are provided with spinous outgrowths. Sporangia are terminal in position and borne on small branch ramifications. It includes *Psilophyton, Dawsonites* and *Loganella*. Andrews and Andrew (1972) reported the presence of 4 distinct species of *Psilophyton* from the trout valley formation in Northern Maine. The two common and often reported species are *P. Princeps* (Dawson) Hueber, and *P. forbesi* Andrews. *Paulophyton Jongmansi* discovered by Krausel in 1957 from Naumurian of Rur hregion also belongs to this family.

4. **Asteroxylaceae.** It includes *Asteroxylon* and the plant body consists of a branched rhizome. Some of the branches function as roots. The aerial stems are covered with leaves. They are simple, oval and slightly dorsiventral. The smaller aerial twigs are naked and spinous. The wood is star-shaped.

5. **Pseudosporochnaceae.** It is typified by a single genus *Pseudosporochnus*. The stem is thick and bulbous below, dividing up above into numerous fine branches. Its appearance is remarkably like that of an alga, but the stem is known to be vascular. The sporangia are oval and borne on the tips of the branches. The branching is dichotomous. Branches that are without sporangia are filiform and most probably serve as leaves.

Family : Rhyniaceae

Genus : *Rhynia* Kidston and Lang.

This genus is named after the locality and possesses two species, *R. gwynne-vaughani* and R. *major*. *R. major* is larger than the former. The genus was discovered in 1913 by Kidston and Lang from Rhynie chert. Accounts appeared in various papers that were published in the Transactions of the Royal Society of Edinburgh.

Rhynia gwynne-vaughani is a small (Fig. 2·1, A) herbaceous plant, possibly about 18 · cmhigh, consisting of slender cylindrical aerial stems and branches arising from a basal rhizome-like portion (Fig. 2·1 A) that was buried in the peat formed by the dead remains of other plants of the same kind. There is not much difference in the structure of the rhizome and the aerial stem except that the former bears at places tufts of rhizoids on its underside. There are no roots and the rhizoids performed the dual functions—absorption and anchorage. The aerial stem is dichotomously branched and tapers gradually towards its apex and is not perfectly smooth but bears a number of hemispherical outgrowths (Fig. 2·1, A). These outgrowths have often been regarded as rudimentary leaves but this interpretation is doubtful. They appeared very late in the life of the plant, usually as new formations beneath the stomata. The aerial shoots may end in pointed tips or they may bear oval sporangia (Fig. 2·1, A, B). Stomata are present all over the surface of the aerial shoots. Adventitious branches also arose from the aerial shoots.

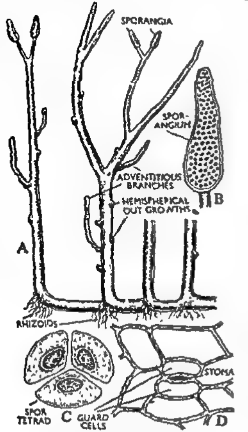


Fig. 2·1 (A—D). Rhynia gwynne-vaughani. A. complete plant showing habit. B. A sporangium. C. A tetrad. D. A stoma.

According to Mercker (1958, 1959) the rhizomatous parts of the plant represent the gametophyte and the upper erect part is the sporophyte. The two evidences that support Mercker's view are: (*i*) the presence of some flask-shaped cavities in the subterranean creeping axis that have been regarded as disintegrated sex organs, and (*ii*) presence of groups of four cells with openings in the centre, in a section of the subterranean part from Munich, resemble the surface view of embedded archegonia. Mercker states that the presence of these groups of 4 cells "reminds us very much of the general type of sunken, more or less neckless archegonia." Similar groups of 4 cells are also present in the pictorial material presented by Kidston and Lang referring to *R. major e.g.*, Fig. 16 in 51 ; 3-4, 1917, Vol. LI. Mercker regards the prostrate regions of *Psilophyton*, *Asteroxylon* and *Rhynia* as richly branched gametophytes. He assumes that the primitive land plants like *Rhynia* must be possessing massive and well developed gametophytes as are found in the present-day eusporangiates (*Lycopodium*).

Another feature of importance in this species is that the hemispherical outgrowths mentioned above were sometimes the seats of the formation of additional branches, quite apart from the normal forking of the stem. Both these structures are absent in *R. Major*. These extra or adventitious branches thus formed were usually without any vascular connection with the main stem. They often become detached and afford a ready means of vegetative propagation. Sometimes these swellings also produced rhizoids.

Internal Structure or Anatomy of the Stem (Fig. 2·2 A)

A transverse section of the aerial stem reveals a distinct epidermal layer interrupted at places by the presence of stomata. The cells of the epidermis also secrete a thick cuticle. Next is the cortical tissue differentiated into an outer and an inner cortex. The cells of the outer cortex are larger than the cells of the epidermis. The inner cortex possesses smaller cells with intercellular spaces between them. These intercellular spaces are connected with stomata through spaces between the outer cortical cells. The inner cortex was most probably the seat of photosynthesis.

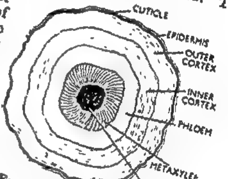


Fig. 2·2. Diagrammatic T. S. of stem showing a protostele.

The centre of the stem is occupied by a vascular strand of a simpler organisation. The centre is occupied by xylem tracheids (Fig. 2·2) that showed traces of annular and sometimes of spiral thickenings. It has also been observed in certain cases that the tracheids in the centre are smaller than the tracheids surrounding them. It reflected on the endarch differentiation of the xylem tissue. The cells surrounding the xylem tissues were thin-walled and without any intercellular spaces. In longitudinal sections these cells appear to be elongated with oblique end walls. This tissue appears to be stelar in nature and is most probably phloem. There are no traces of sieve plates or pores in the cells of phloem and it is in this respect that this tissue differs from the phloem of the living Pteridophytes. Satterthwait and Schopf (1972, 373-376) reported the occurrence of numerous pores (3—8 μ in diam.) distributed along the latter cell walls in this zone of tissue. In face view these pores appear to be composed of circular sub-units. They reported the presence of sieve tubes and parenchyma cells in the phloem zone and also observed the presence of pit fields in the lateral cell walls and inclined end walls of sieve tubes. The pericycle and endodermal layers were lacking.

In the rhizome there is no distinction between the outer and inner cortex and the xylem strands consist of but fewer tracheids.

The growing point consists of numerous dividing cells. There is no apical cell.

Sporangia. They are club-shaped or cylindrical structures (Fig. 2·1) borne terminally on the fine aerial branches (4 m.m. long and 1·4 m.m. broad). Their wall is three layered : an outer epidermal layer, a middle three cell rows thick layer and an inner layer. The outer layer is heavily cutinised. The sporangium contained large number of spores arranged in tetrads like the modern ferns. They are homosporous and measured 40 μ in diameter. The spore wall must have been tough so as to preserve them

layer and an inner layer of primary sporogenous cells.

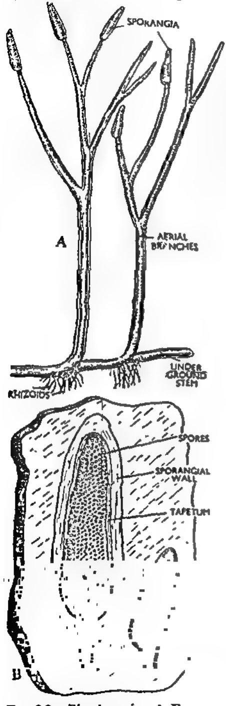


Fig. 2·3. *Rhynia major*. A. Reconstruction of a complete plant B. sporangia.
(After Kidstone and Lang).

RHYNIA MAJOR

It is wholly a leafless plant

of any hemispherical outgrowths as are found in the other species.

about 12 mm. long and 4 m.m. in breadth.

Internal structure too is very simple and agree in all respects to that of *Rhynia gwynne-vaughani*. Stele is a typical protostele,

are the points that differentiate this species from the smaller *Rhynia gwynne-vaughani*.

Pant (1960) regarded the small-sized *R. gwynne-vaughani*

to be the gametophytic part of *R. major* because :—

(*i*) The sporangia assigned to *R. gwynne-vaughani* were not found in organic connection with this plant and might have been the immature sporangia of *R. major*.

(*ii*) The hemispherical bulges and the adventitious shoots of *R. gwynne-vaughani* were the young embryos that were clearly demarcated from the main axis and possessed haustorial cells, like those present in the foot of the young embryos of *Psilotum*.

The chief arguments against such an interpretation are :—

(1) Absence of definite sex organs in connection with the axis. In case embryos could be preserved there should have been no difficulty for the sex organs to be preserved (Mehra, 1968).

(2) Presence of stomata with guard cells on the axis.

(3) Presence of a vascular strand.

Horneophyton (=*Hornea lignieri*)

This is as simple a plant as *Rhynia* and was discovered from the same chert bed. It is much smaller in size and shows certain characteristics of great importance and singular interest. The aerial shoots are only two millimetres in diameter and arise from a more or less tuberous or swollen rhizome, from the underside of which arise numerous rhizoids. The aerial shoots are leafless, naked and dichotomously branched. The rhizoids are nonseptate.

Anatomy of the aerial stem is the same as in *Rhynia* but differs in the rhizome. The xylem of the vascular cylinder of the aerial stem terminates in the upper part of the tuberous rhizome in a group of approximately isodiametric cells, the walls of which have the same colour as the tracheids, in contrast to the other cells of the rhizome which appear to have been parenchymatous. So there is no vascular tissue in the rhizome itself. More than one shoots arise from the rhizome but without any vascular connection.

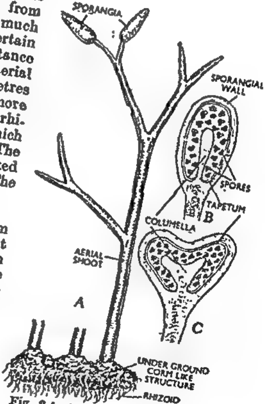


Fig. 2·4. **Horneophyton lignieri.**
A. A complete plant.
B. A normal sporangium with columella.
C. An abnormal dichotomously branched sporangium.

The sporangium or the fructification of *Horneophyton* is of chief botanical interest and remarkable in more than one ways.

The sporangia are borne terminally upon certain branches of the stem. There is very little differentiation in the wall, although it is thick. A well defined tapetum could no doubt be recognised over-arching a central columella (Fig. 2·4 B, C). In fact the sporangia are nothing but enlarged tips of the branches. In certain cases the sporangia too are dichotomously forked (Fig. 2·4, C). This is a point of interest that shows that the sporangium is not a distinct organ but just the end of a branch, modified for spore bearing purposes.

Another important sporangial feature is the possession of a central sterile column of cells called the **columella.** So it may be added that the spore bearing layer overarches the columella, recalling the situation met with in *Sphagnum*-like mosses. This feature has strongly suggested that *Horneophyton* and its alies, though vascular in nature, may have had affinities with the moss stock.

In the forked sporangia the columella too is forked (Fig. 2·4.C) The spores are formed in tetrads and are 50μ in diameter. The cells of the columella are elongated and continuous with the phloem of the stem below It served for the conduction of food as in the recent plants. Tapetum is a nourishing tissue for the developing spores.

Brief account of the other members of the family Rhynicaeae

1. **Sporogonites exuberance.** This is another fossil, from Norway, of lower Devonian age, and was described by Dr. Halle. The plants are smaller in size, the stem is naked and the sporangia terminal. The sporangium is much more like the moss sporangium. It is not more than 9 mm in lengths and the diamster varies from 2 to 4 mm. There is a well developed columella made up of slender cells, occupying the base of the sporangium and extending right in the centre as a column of sterile cells. It is distinctly overarched by a sporogenous layer. The spores are formed in tetrads. Their diamenter varies from 20 to 25μ. Regarding the mechanism of dehiscence, nothing is known as yet.

In the stem no trace of vascular strand is seen. The absence is most probably due to faulty preservation. It makes the position of *Sporogonites* doubtful. The resemblance of the sporangium with a moss capsule and absence of vascular strand places *sporogonites* among the Bryophytes. But no member of Bryophytes has been reported from the Devonian age with certainty so *Sporogonites* is placed in Psilophytales, closely resembling *Horneophyton.* If presence of vascular system is reported the assignment to Psilophytales becomes sure. The discovery of *Horneophyton* and Halle's *Sporonites* have thrown much light on the analogy of these early vascular plants with the mosses. This is a point of considerable interest, for previously the fossil record has failed to throw any light on the history of the Bryophytes.

Another species of the *Sporogonites* discovered in the upper Silurian of Australia is *Sporogonites chapmani.*

2. **Cooksonia.** It was found in the lower Devonian of Wales (Lang, 1937) but has not been fully worked out. There are two species, viz., *C. hemispherica* and *C. pertoni.* The stems are naked, straight and dichotomously branched. These features relate it to *Rhynia.* The spore sac is much broader than long. The upper surface is more or less rounded. Much less has been known regarding the anatomy of the stem and the internal structure of the sporangium. The sporangium is terminal no doubt. It has also been discovered from Bohemia by Obrhel (1962.)

3. **Yarravia.** Lang and Cookson discovered the fructification called *Yarravia* in 1935 from Monograptus beds of Australia. These beds have been estimated to belong to the middle Silurian period. The chief point of interest

lies in the fructifications that are closely joined together at the base but free at the ends. Three to five oval sporangia have been discovered in lateral union as above. These sporangia are borne terminally on a smooth, straight and leafless stalk. There are tow species differentiated with respect to the shape and size of sporangia. These species are *Y. subspherica*, *Y. oblonga*.

4. **Hicklingia.** It was discovered in Caithness in Scotland in the [illegible] ot rhizomatous portion [illegible] ously. The branching [illegible] ngia are terminal and [illegible] leafless and about 15 cm. long and about 3 mm. in diameter.

DISCUSSION

In the words of Dr D.H. Scott, «the Rhyniaceae, simple as they are [illegible] aracters pre- [illegible] linary posi- [illegible]

Rhyniaceae can very well be treated as a synthetic group of plants combining the characters of vascular cryptogams and the bryophytes on one hand and retaining some of the characters of the thallophytes on the other side. Such a conclusion is justified by the structural facts actually known to us. The question arises whether the Rhyniaceae were really primitive plants. Their environments were quite unfavourable and it is just possible that the plants became reduced due to environmental stresses. Whatever the case may be the facts remain that Rhyniaceae are a group of simplest and the ancient of the plants known to us.

Out of the living Pteridophytes the Rhyniaceae bear resemblances with the Psilotales. The order includes two living representatives, *i.e.*, *Psilotum* and *Tmesipteris*. The aerial stems of *Psilotum* are devoid of true leaves like *Rhynia* and are in the same fashion, dichotomously branched. There are no roots. The underground rhizomes are provided with tufts of unseptate rhizoids. *Tmesipteris* does bear leaf-like appendages but they are flattened lateral y and merge with the stem by strong decurrent bases. the sporangia are borne on shor t branches that arise laterally from the stem.

The bulbous rhizome of *Horneophyton* recalls the protocorm of some members of the Lycopodiales, *e. g.*, *Phylloglossum*. Protocorms always develop before the roots and are connected to the soil by means of rhizoids, [illegible]

opinion is that the early pteridophytes (Psilophytales) had an algal ancestor rather than a bryophyte.

[illegible] Bryop [illegible] gonite [illegible] Bryop [illegible] to the [illegible] coverc [illegible] has been found out.

Smith has drawn a line of similarity between the tuberous rhizome of *Horneophyton* and the foot of some species of *Anthoceros*. Anthocerotean sporophyte has been very closely homologised by the supporters of this view. They believe that the *Rhynia* like sporophytes have originated from sporophytes of *Anthoceros* The sterile region between the sporangium and the tuberous rhizome of *Horneophyton* has developed by the further sterilization of the tissue above the foot of the sporophyte of *Anthoceros*. This sterile elongated portion developed vascular system that is not present in *Anthoceros*. The sporophyte of *Anthoceros* has several layers of wall and the cells contain chlorophyll so that they can manufacture food. Stomata are also present in the epidermis. However the sporophyte of *Anthoceros* is partly parasitic on the gametophyte But there is every possibility that if called upon ... independently the *Anthoceros* sporophyte can survive ... experimentally by Dr. Campell. He ... and grew them success... ... ancestral forms of the first vascular plants were in their ...

More recent views believe in the origin of both bryophytes and pteridophytes from a common stock, most likely from algae with alternation of generations, since this is shown by all Archegoniatae. No higher plants can be derived from the bryophytes; they form a blind alley of evolution. Bryophytes and Pteridophytes form parallel branches of the evolutionary tree, stemming from a common green algal ancestor. Such an ancestor belonged most probably to the heterotrichous Chaetophorales.

Family : Asteroxylaceae

It is represented by the single genus *Asteroxylon*. This genus is represented in the middle Devonian period by two species, *viz.*, *A. mackiei* and *A. elberfeldense*. They were discovered in the Rhynie valley. The latter species was found in the middle Devonian near Elberfeld in Germany.

A mackiei was reconstructed from several fragments of the fossils of the same plant. The complete reconstruction gives the idea of its external morphology. The rhizomes are smooth and bear slender branches that functioned as roots. The rhizomes are dichotomously branched and some of the slender branches that penetrated the substratum are regarded as roots. The aerial stems are leafy and arise from the rhizome. There is a transition region between the smooth rhizome and the aerial leafy shoot. On the transition region there were small scales without any traces of vascular strands developed in relation to them. On the aeral parts, however, a vascular strand is present in connection with the xylem of the shoot which extends upwards through the cortex as far as the base of each leaf into which, however, it does not extend. The leaves are dorsiventral and oval in section.

The aerial stem branched laterally and these branches forked dichotomously (Fig. 2·5, A). Dichotomy has also been recorded in the main stem. The diameter of the stem is about 1 cm. near the base. It is 1 mm. in the outer extremities of the stem. The leaves ...re 5 mm in length and have stomata distributed among the epider... cells. There is a well defined cuticle too in the leaves. The

leaves go on becoming smaller towards the base and finally merge with the scale leaves of the transition zone.

Anatomy

Xylem in the stem is deeply fluted and appears star-like in structure (Fig. 2·5, B). The tracheids at the ends of the xylem rays are smaller than those at the centre. This shows exarch arrangement.

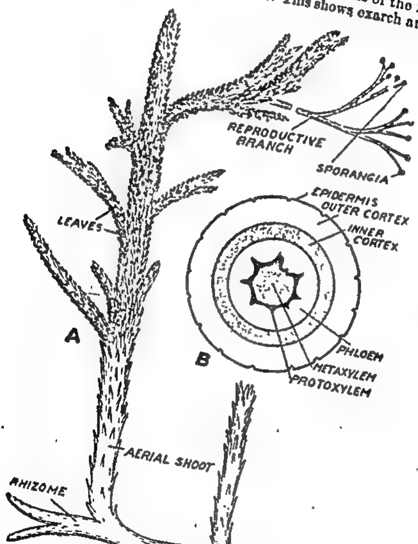


Fig. 2·5.
A. Reconstruction of *Asteroxylon mackiei*.
B. T.S. Stem showing actinostelic–protostele.

The tracheids are spirally thickened and show an annular thickening *in the smaller tracheids. The phloem extends as a thin layer all round* the xylem. Indications of the presence of ill-defined endodermis are also found in some specimens. The stele is *actinostelic.*

In the rhizome the xylem is cylindrical and rod shaped and is *composed of tracheids. There is no distinction into proto* and metaxylem. It is surrounded by phloem.

[illegible] Presence of [illegible]

thr[illegible] [illegible] Usually it is composed of un[illegible] cortex are more or [illegible] *where the cells* are trabaculate. The inner cells of the inner cortex are also compact. Presence of fungal hyphae has also been reported from the cortical cells. They are attributed to the genus *Paleomyces.*

Spore Bearing Members

It is unfortunate that the evidence as to the reproductive organs of *Asteroxylon* is less satisfactory than in the case of *Rhynia* and *Horneophyton*, for the fructifications attributed to the plant have never been found in connection with it. Peculiar naked branches, quite different from the vegetative stem, have been found in close association with some specimens; and associated with these doubtful branches sporangia have been observed. They are usually different from those of Rhyniaceae and rather resemble the spore sacs of certain carboniferous ferns. The sporangia thus attributed to *Asteroxylon* have a definite dehiscence like fern sporangia while no such provision exists in the Rhyniaceae.

Dr. D.H. Scott remarked, "I cannot undertake to say whether the reproductive organs provisionally assigned to *Asteroxylon* really belonged to the plant or not. It looks as if they did, but there is no proof."

The uncertainty regarding the fructifications of *Asteroxylon* leaves the affinities of the plant quite doubtful.

The sporangia are pear-shaped and one millimetre long and are borne on long, naked, branched axes. *Asteroxylon* is homosporous and the diameter of the spore is 64μ. These fructifications have [illegible] (1964). Lyon (1964) [illegible] *ackiei*. He has found [illegible] ngia borne on short [illegible] among the leaves. [illegible] can now no [illegible] *ylon* because it [illegible] d fertile shoot. [illegible] ated stele and [illegible]

Asteroxylon is slightly advanced than other members of the Psilophytales in possessing leafy stems and star shaped xylem with distinction into proto-and metaxylem.

Anatomically and to some extent in its habit, *Asteroxylon* is homologous with *Lycopodium*. The rootless rhizome, the simpler fructifications are characters suggestive of Psilophytean characters. The branched aerial shoot too represents the Psilophytean character.

CHAPTER III

Division : PSILOPHYTA

Class : PSILOTOPSIDA

Order : PSILOTALES

Family : *PSILOTACEAE*

The order Psilotales is closely related to the extinct order Psilophytale[s] and comprises two genera. These are *Psilotum* and *Tmesipteris*. Both thes[e] genera are placed in the family *Psilotaceae* and possess two species each. I[t] has now been proposed to refer *Tmesipteris* to a separate family *Tmesipteri*daceae.

PSILOTUM

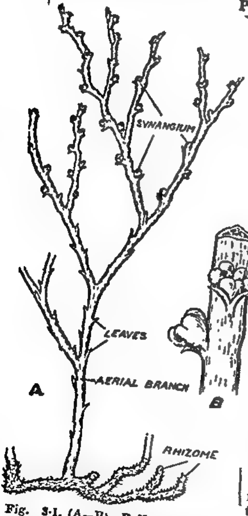


Fig. 3·1. (A—B). **Psilotum nudum.**
A. A complete plant showing habi.
B. Part of stem bearing synangia.
(B. After Pritzel).

Distribution. It grows as an epiphyte in tropical and sub-tropical regions of the world and is abundant in Florida, Bermuda, Jamaica, Mexico, a few Pacific Islandsand Hawai islands. In India it has been collected from Bengal, Assam, Pachmarhi hills, Kulu (Himachal Pradesh) and Madhya Pradesh. At Kulu it has been found growing from the crevices of rocks and on soil. *Psilotum nudum*(=*P. triquetrum*) and *P. flaccidum* (=*P. complanatum*) are the only species discovered so far. The terestrial forms of *P. nudum* grow erect and are dwarf, whereas the epiphytic forms grow pendent (75—100 cm. high). *P. flaccidum* differs from *P. nudum* in possessing flattened stems.

Plant Body. The plant body is distinguished into two parts (Fig. 3·1) : (A) Rhizome which is mostly hidden below the humus (epiphytic species) or the soil and is dichotomusly branched and bears scales. The rhizome lacks roots, harbours an endophytic fungus and bears numerous filamentous rhizoids that per form the twin function of anchorage and absorption. Bierhorst (1954) is of the opinion that branching of the rhizome is dependent upon the type of obstacles encountered by its

main site of photosynthesis

growing tips. (B) An erect or pendent green aerial portion, which

ribbed. Near the upper region the aerial stems show three longitudinal ridges. The apical meristems of both the rhizome and the aerial stems consists of a single tetrahedral apical cell with three cutting faces. (Ford, 1904; Marsden and Wetmore, 1954; Berhorst, 1954).

Anatomy of Stem. The outermost boundary of stem is formed by a single layered epidermis with thick outer walls. The epidermis is lined by a layer called cuticle which is made up of cutin and waxes. It is secreted by the epidermal cells and extends into the stomatal pore. The stomata have no subsidiary cells and have two prominent outer ledges (Fig. 3·3). They are restricted to the grooves between longitudinal ribs.

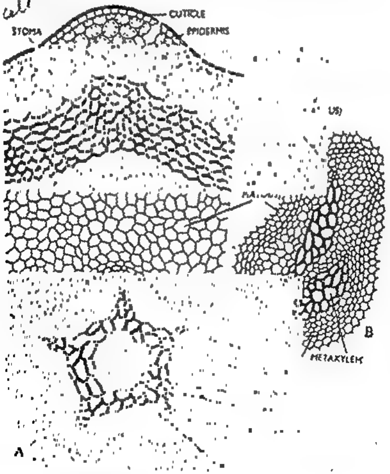


Fig. 3·2. *Psilotum nudum.* A. T. part of aerial stem near the upper region showing actinostele.
B. Portion of T.S. of stele of aerial stem cut near the apex.

Cortex. It is differentiated into three well marked regions (Fig. 3·2, A).

1. The outer cortex which is composed of thin-walled slightly lobed, loosely arranged and chlorenchymatous, elongated cells. The cells may contain starch grains.

2. The middle cortex is composed of vertically elongated chlorophylless cells that have thickened cell walls and enclosed comparatively smaller intercellular spaces. They contain few or no starch grains. In the basal portions of the aerial stems this region is composed of lignified cells.

3. The inner cortex is composed of several layers of cells which show gradual reduction of the thickness of cell walls as we proceed towards the stelar region. The cells contain starch grains. This region is also called the storage region.

The endodermal cells have distinct casparian strips. The pericycle is single layered and consists of three walled cells.

Vascular Region

The vascular region is surrounded by a single layer of pericycle and an endodermis. It consists of xylem and phloem ; the latter completely surrounds the former. The following variations in the vasculature of rhizome and at various levels of aerial branches were observed by Bower (1935) and Pilot (1950) :

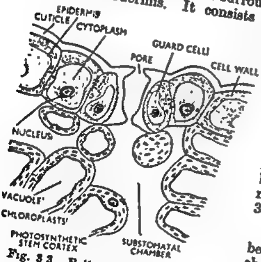


Fig. 3·3. *Psilotum nudum*. T. S. portion of stem showing epidermis and stoma.

(*i*) In the rhizome it is a protostele with central core of xylem completely surrounded by phloem. The xylem core is not star-shaped or lobed (Fig. 3·3). There is no pith.

(*ii*) In the transit zone between rhizome and aerial shoot the xylem becomes lobed and as many as 10 lobes can be counted. There is no pith. The protoxylem occupies the tips of the lobes. The phloem occurs in between the lobes and forms irregular patches. Here the stele is actinostelic protostele.

(*iii*) In the middle of aerial shoot the number of xylem lobes is reduced to 5 or 7 and pith appears in the centre (Fig. 3·2, A). Here it changes from protostele to a siphonostele.

(*iv*) In the apical regions of the aerial shoot the outline of the stele is triangular and the xylem splits into two distinct patches.

In all these cases the xylem is **exarch.** It consists of only tracheids. The protoxylem has spiral tracheids whereas the metaxylem tracheids are scalariform or pitted. The phloem consists of sieve tubes and phloem parenchyma. The sieve tubes are vertically elongated with slight lignification at the angles and have sieve plates in both lateral and terminal walls. They lack nuclei at maturity, but some spherical bodies have been reported in the cells (Ford, 1904, Stiles, 1910, Esau, 1953).

In the region of the rhizome a transverse section reveals a well defined epidermis (Fig. 3·4, A), followed by a broad zone of cortex. The cortex has an outer mycorrhizic zone (Fig. 3·5), middle zone of starch storing cells and an inner cortex whose cells contain phlobaphene. There is a distinct endodermis surrounding a single-layered pericycle which in turn encircles the protostele (Fig. 3·5). The protostele has a central core of exarch xylem surrounded completely by phloem.

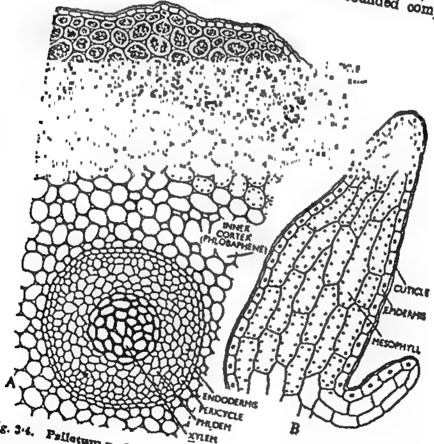


Fig. 3·4. *Psilotum nudum* A. T. S. portion of rhizome, B. L. S. leaf.

Anatomy of the leaf

The leaf is merely an emergence without a vascular supply. It is made up of chlorenchymatous cells surrounded by an epidermal

layer devoid of stomata and chloroplasts (Fig. 3.4, B). The chlorenchymatous mesophyll is continuous with chlorenchymatous outer cortex of the aerial stem. In *P. flaccidum* a leaf trace ends at the base of the leaf like emergence.

Vegetative Propagation of the Sporophyte

Holloway (1939) and Bierhorst (1954) reported the presence of minute, ovoid and multicellular outgrowths arising amidst the rhizoids on the rhizome of *Psilotum* [illegible] brood bodies [illegible]

Each gemma grows by means of a two-sided apical cell. Its cells are thin-walled [illegible]

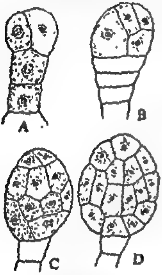


Fig. 3.5. Gemmae or Brood bodies from the rhizomes of Psilotum nudum.

Reproduction by Spores

Spores are produced in specialised bodies called the **sporangia or synangia** that appear on the aerial shoots (Fig. 3.1, A, B).

Sporangia

Structure. [illegible] *Psilotum* are not terminal but [illegible] 3.1, B) associated [illegible] through the three lobed sporangium reveals that [illegible] into three sporo- [illegible] spore mother cells [illegible]

Dehiscence. [illegible] three apical [illegible] sporangial [illegible]

Development : The development of the sporangium is of the eusporangiate type. According to Bower (1935), the sporangium arises as an outgrowth [illegible] side of the bilobed

[illegible]

appendage which arises later as a lateral outgrowth from the sporangial stalk. Biehorst describes the development as follows :

Each lateral outgrowth destined to develop into a trilobed sporangium, grows by means of an apical cell to form a short multicellular fertile axis (stalk of sporangium). Three separate surface initials make their appea- [illegible]

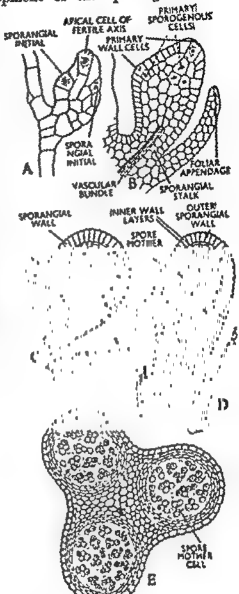


Fig. 3·6. (A—E). Psilotum nudum. A—D. Stages in development of sporangium. E. Mature synangium showing three loculi. (After Bower).

The sporangial stalk and the partition walls between the sporangial locules are traversed by a vascular strand, which does not extend into the foliar appendages.

Morphology of the Sporangium

Three divergent views have been advanced to interpret the spore producing structures in *Psilotum*. According to one view the trilobed sporangium is regarded as a synangium, *i.e.*, it is considered to be a fusion product of three sporangia (Bierhorst, 1956). The second view regards the forked appendage as the sporophyll bearing a trilocular sporangium. This view was put forth by

Solms-Laubach (1884) and was supported by Bower (1908), Schoute (1938), Seward (1910) and Velenovsky (1910). The third view regards the sporangium as occupying a terminal position on a short lateral branch. According to this view the sporangium is trilocular and cauline in origin with a terminal position. This view was advanced by Juranyi (1871) and was supported by Sachs, Strasburger and Goebel. Eichler also supported this view.

Presence of a vascular strand in the sporangium supports its being axial in position.

Some regard the sporangial stalk as comparable to the ... in the equisetales.

Bierh... with the ... gards the ... leaf-like a... sed structu... the spore ... archesporia... observed th... locules. Th... gium is act... ...nclude that the trilobed sporan... formed by the fusion of three sporangia.

Gametophyte Generation

It starts with the spore and has been described by Darnell Smith (1917) and Bierhorst (1953) in *P. nudum*.

The Spore. *Psilotum* is homosporous. The spore tetrads may be tetrahedral or even isobilateral. The two curved ends of the mature kidney shaped spores are joined by a narrow **ridge** traversed by a median **slit** that runs along 3/4 of its length (Fig. 3·7, B). The slit is bordered on either side by a thick and smooth border called the **lip**. The spore has an outer thin and reticulate **exine** and an inner **intine**. It is uninucleate, about 0·65—0·32 mm. in size and with granular and food-laden cytoplasm. The exine is **spinulose**. The spore is monolete.

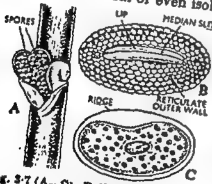


Fig. 3·7 (A—C). Psilotum nudum. A. Showing a dehiscing sporangium; B. A spore; C. A spore seen in optical section. (A and B after Wettstein; C after Darnell Smith).

Germination of spore

The spores germinate very slowly and it takes 3 to 4 months for a spore to germinate in artificial cultures. The earlier stages of germination (Fig. 3 8) as studied by Darnell Smith (1917) can be listed as below:

1. The exine ruptures along the median slit.

2. The intine protrudes out as a small globular outgrowth which gradually increases in size.

3. The protruded part is later separated from the basal part, which is within the spore wall, by a transverse wall. The young prothallus at this stage consists of two cells (Fig. 3 8, B).

4. The upper or the exposed cell divides obliquely to cut off an apical cell (Fig 3 8, C). Holloway (1939) reported the apical cell to have four cutting faces but Bierhorst (1953) observed it to be a pyramidal cell with three cutting faces.

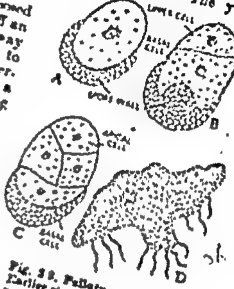


Fig. 3 8. Psilotum nudum. Earlier stages of spore germination. (After Lawson).

5. By the activity of the apical cell a mass of thin walled cells is formed (Fig. 3 8, D). They are devoid of chlorophyll and are attacked by an endophytic fungus at this early stage.

Further stages of development have not been studied.

Mature Prothallus (Fig. 3 9, A, B)

The gametophytes grow as saprophytes with an associated endophytic fungus which gains entry through the rhizoids. The fungus is probably *Cladochytrium tmesipteridis*. The gametophyte is a cylindrical, imperfectly dichotomously branched structure with a diameter ranging between 5 to 6 mm. The fully grown gametophytes are up to 20 m m. long. Under natural conditions they are found growing in the crevices of the rocks or on the trunks of trees. They are colourless or yellowish brown in colour. Numerous rhizoids arise from the surface of the gametophyte.

The prothallus is mostly composed of hexagonal cells that are devoid of chloroplasts. The cells are strongly cutinized along their outer and radial walls. The outermost layer of cells gives off rhizoids at frequent intervals. The rhizoids are short, filamentous outgrowths that are two or three cells in length. Holloway (1938, 1939) and Bierhorst (1953) have recorded the presence of well defined, scalariform or scalariform-reticulate tracheids, surrounded by phloem and endodermis in the centre of the prothallus. Such a vascular strand is a characteristic feature of the sporophyte and their presence in the gametophyte of *Psilotum* raised interest in the minds of botanists. Cytological investigations have revealed that the prothalli with such a vascular strand are diploid. Manton (1950) has recorded a wild growing diploid gametophyte from Ceylon. The haploid chromosome number for *Psilotum* has been reported to be 52-54, whereas prothalli with 100 chromosomes have also been reported (Bierhorst, 1953) in a race of *Psilotum*. This indicates that polyploidy is common in *Psilotum*. Such polyploid gametophytes have also been reported in other pteridophytes (ferns), but the presence of a distinct and well differentiated vascular strand in the prothallus is an unusual character. Holloway (1939) studied the growth of prot

in *P. nudum*. and described the occurrence of interrupted vascular system that was essentially a protostele. He found that the protostele was periodically interrupted by intervening regions of parenchyma. Holloway found that growth in these prothalli was inter-

Fig. 3.9. *Psilotum nudum*. A. Mature gametophyte ; B. T. S. mature gametophyte showing red organs and a central vascular strand ; C—D. Gametophyte gemmae.

A mature antheridium (Fig. 3·10, G, H) is more or less a globular structure without any stalk. It consists of a *single layered wall* with enclosed spermatocytes.

Archegonium. It develops from a single superficial cell (Fig. 3·11, A) which divides periclinally into an **outer cover cell** and an inner **central cell**. The cover cell divides by two intersecting anticlinal walls to form four cells, which act as initials of the four rows of the archegonial neck (Fig. 3·11, C). These four cells divide by repeated transverse walls to form four longitudinal rows of the neck, each row from 4—6 cells high. **The central cell divides** (when the neck is only three cells long) by a transverse wall into an upper **primary canal cell** and a lower **primary ventral cell** (Fig. 3·11, D). The former divides by a transverse wall to form two neck canal cells. In most cases the wall separating the two neck canal nuclei has *not* been observed (Fig. 3·11, E). **The primary ventral cell divides transversely** (Fig. 3·11, F) into an upper **ventral canal cell** and a lower **egg cell.** Bierhorst (1954) has reported a case where the central cell functions directly as the egg cell.

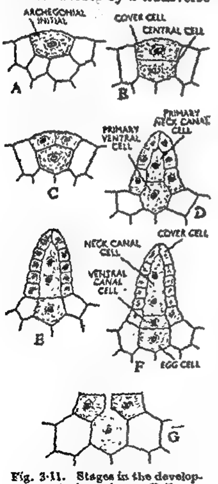


Fig. 3·11. Stages in the development of Archegonium in *Psilotum nudum*. (After Bierhorst)

The necks of the archegonia are straight, and the *venter is embedded in the tissue of the gametophyte.*

A mature archegonium consists of *4 longitudinal rows of neck cells,—each row 4 to 6 cells high.* The neck encloses a neck canal (Fig. 3·11, F) with two **neck canal nuclei** or two **neck canal cells.** *There is a single* **ventral canal cell** and a single **egg cell.** There is no sterile wall surrounding the venter as this portion is embedded in the tissue of the gametophyte.

As the archegonium matures the cell walls between upper tiers of neck cells become cutinised and the upper part of the neck breaks away (Fig. 3·11, G).

Bierhorst (1954) states that this breaking off of the neck takes place after the process of fertilisation. Earlier workers believed it to have taken place before the act of fertilisation.

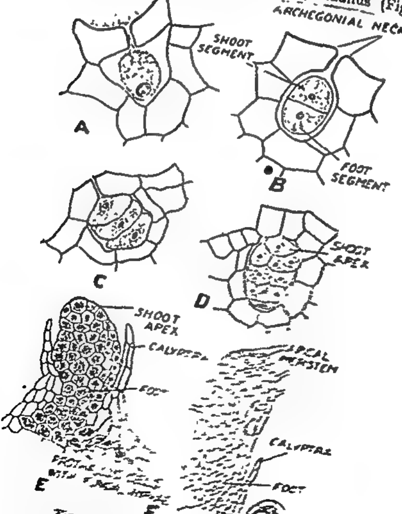
Prior to fertilisation, it appears, the usual disintegration of the axial row of cells (neck canal cell and ventral canal cell) takes place.

They absorb moisture, become mucilaginous and force open the uppermost tier of neck cells thus permitting the spermatozoids to enter the archegonial neck and reach the egg.

Fertilisation consists in the union of spermatozoid and the egg, followed by the fusion of the male and the female nuclei (syngamy). There is every possibility that fertilisation may not even take place in the diploid or the polyploid gametophytes.

Vegetative Propagation of the Gametophyte

Holloway (1939) and Bierhorst (1953) reported the development of gemmae on the surface of the prothallus (Fig. 3·7, E, F).



[illegible] *Psilotum nudum.* [illegible]

They appear [illegible]
The terminal [illegible]

to form an ovoid gemma-like structure that may contain 8·12 cells at maturity. These gemmae germinate to give rise to new prothalli. In addition to gemmae Holloway (1939) reported the formation of small outgrowths which develop from one or two surface cells that divide to form bud-like outgrowths. He named them as **vegetative buds.** They differ from gemmae in their mode of origin. They do not arise on the tips of short outgrowths but directly on the prothallus.

The Embryo

The zygote divides first by a transverse wall into an **epibasal cell** or **shoot cell** (Fig. 3·12, B) towards the neck of the archegonium and a **hypobasal cell** or **foot segment** below. The epibasal cell gives rise to the shoot system (both rhizome and the aerial branches) and the hypobasal cell divides in various planes to give rise to a bulbous foot which gives out haustorial out-growths into the gametophyte (Fig. 3·12, C—E). It secures the sporophyte to the gametophyte and absorbs nutrition from it till the sporophyte becomes independent. While the foot is developing the epibasal cell divides in three different planes (Fig. 3·12, C, D). A three sided apical cell of the young sporophyte soon differentiates at the tip of this outgrowth (Fig. 3·12, D). At this stage the embryo bulges out as a prominent outgrowth on the surface of the gametophyte (Fig. 3·12, E). As a result of the activity of this apical cell the shoot soon grows vertically and becomes prominent. The surrounding cells of the gametophyte divide to form a calyptra-like outgrowth enveloping the young embryo. By further growth the embryo pierces through the calyptra (Fig. 3·12, E, F). The young shoot soon establishes itself as a young axis with vascular tissue. It is the future rhizome which is at first unbranched, but undergoes branching at a later stage. The young rhizome detaches itself from the foot by the formation of a separation layer at the original boundary between the foot and the shoot.

The rhizome contiunes to grow in length and branches repeatedly in a dichotomous manner. The tips of the ultimate branches turn upwards and develop into aerial branches that come out of the humus and grow erect.

The embryo of *Psilotum* is remarkably differnt from most of the other. pteridophytes in lacking initials of suspensor, leaf and root.

Distinct Features of the Prothallus

1. The gametophytes of the Psilotaceae are subterranean. 2. The colour is light brown or dark brown. 3. The lack chlorophyll. 4. The body is usually cylindrical. It branches and each branch has a terminal meristem. 5. The prothallus tissue is uniform except the epidermal layer that is quite distinct. 6. Presence of tracheidal cells or even distinct vascular strands—a unique feature of the Psilotaceous gametophyte. 7. The prothallus is saprophytic and is attacked by an endophytic fungus. 8. Surface of the prothallus is beset with numerous unicellular rhizoids. 9. The prothallus is monoecious. 10. The sex organs are irregularly distributed and intermingled. 11. The spermatozoids are multiflagellated. 12. The

antheridia bulge above the surface of the prothallus. 13. The archegonial neck is composed of four longitudinal rows of cells and projects above the surface of thallus. The venter is embeded. 14. Disorganisation of the tiers of neck cells.

Affinities of Psilotales

Regarding the affinities of this group there are still doubts in the minds of botanists. Four theories have been put forth to explain the position of the group:

1. Kidston and Lang (1917—1921) propounded a theory suggesting close relationship between Psilotales and the Psilophyatales. This theory is also supported by Holloway and Bower.

2. Arber suggested their late origin along independent lines from the algae.

3. The hypothesis maintained by A.P.W. Thomas and formerly *suggested by Bower and Scott, of an affinity with the Sphenophyllales.*

4. The old fashioned view that Psilotales are essentially Lycopods (Lawson, 1917).

Considering the first theory, the Psilotales resemble the Psilophytales in : (*i*) having rootless rhizomes, (*ii*) protostelic stem, (*iii*) small size of the leaves, and (*iv*) dichotomously branched shoots.

They differ only in the position and number of sporangia. Kidston and Lang pointed out that not only do the Psilotales resemble the fossil [illegible] members of the Psilotales are living remnants of Devonian flora that has come down to the present day without much change from the very ancient times.

Lawson (1917) expresses himself favourably towards the affinity with the sphenophyllales while pointing out that the gametophytic generation can offer no positive evidence.

Affinity with Sphenophyllales is ruled out because there are many important differences between them and the Psilotales. The leaves in Sphenophyllales are whorled as compared to spiral arrangement in the Psilotales. The branching in the Sphenophyllales is monopodial as compared to the dichotomous branching in the Psilotales.

Regarding their affinities with the Lycopods as suggested by Lawson [illegible]

Arber agrees with Thoday and others in that the Psilotales are an entirely distinct group from either the Lycopods and the Sphenophyllales. Arber regards it as quite an independent race had an algal ancestor.

[illegible]

1. The axial gametophytes are underground. 2. The underground sporophytic stem and the gametophytes are indistinguishable in both. 3. The gametophytes bear septate rhizoids in both. 4. Alternate periods of growth in both the sporophyte and the gametophyte produce short and long cells. 5. The archegonia in both the families dehisce by the decapitation of the neck. 6. Sporophytes are rootless. 7. Spores are monolete. 8. Similarities in the development and wall structure of the sporangia. 9. The terminal leaf of *Tmesipteris* and terminal pinna of *Stromatopteris* develop from the apical meristem and consume it. 10. Large superficial antheridia with lateral opercular cell which breaks down at maturity. Discontinuous vascular tissue in smaller axes of the sporophyte. 11. Synchronous xylem maturation in smaller subterranean stems. 12. Mesarch xylem [illegible]

14 [illegible]

families 15. Nucleoli at mitosis persisting up to anaphase stage.

Bierhorst regards the aerial axes of *Psilotum* and *Tmesipteris* as fronds.

Significance and Phylogeny of Psilophyta

The affinities of the two classes of Psilophyta have been discussed in detail in the relevant chapters. The division Psilophyta is of great evolutionary significance as it includes two closely related classes of extinct and living plants (Psilophytopsida and Psilotopsida). They are the oldest known and [illegible] either leafless or possess [illegible] connecting links between [illegible] plex vascular plants like [illegible] lophytales resemble some [illegible] b) absence of leaves; and (c) absence of roots. They differ from algae in possessing : (a) definite cuticle; (b) stomata; (c) cutinised spores and (d) a vascular system with well defined xylem and phloem.

This division of plants offers a number of evidences that have a great evolutionary importance. These can be listed as below :

1. They throw light on the origin of root, as suggested by Prof. Lignier [illegible] and entered [illegible] nchorage and [illegible] ophytales and [illegible] beneath the [illegible]

2. They also suggest the origin of microphyllous and megaphyllous leaves of lycopods and Ferns. The leaf-like emergences of *Asteroxylon* and *Psilotum* might have developed into small single veined and microphyllous leaves of the Lycopods. In *Pseudosporochnus* and *Protopteridium*, the leaves are formed by flattening of the branch system and are supposed to have led to the development of larger and megaphyllous leaves of ferns.

3. The anatomy of the shoot in the Psilophytales also suggest that protostele is the primitive type of vasculature and that siphonostele has originated from it by the appearance of pith. It also suggests that the annular tracheids are the simplest and the spiral and scalariform tracheids are advanced.

4. A comparative study of the Psilophytales and the higher vascular plants also suggest the establishment of four distinct subdivisions, namely, the Psilopsida, Lycopsida, Sphenopsida and the Pteropsida. The Psilophytales indicate clearly the three lines of evolution which lead to the development of Lycopsida, Sphenopsida and the Pteropsida (Fig. 3-17).

Certain members of the Psilophytales, e.g., *Asteroxylon* possess small leaves that arise as emergences and might have given rise to the Lycopsid line

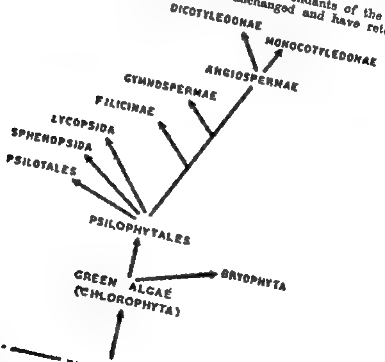
Some Psilophytales such as *Hyenia* clearly indicate a tendency towards the whorled arrangement of the branches and might have given rise to the Sphenopsida.

A few Psilophytales, *e. g.*, *Pseudosporochnus* and *Protopteridium* exhibit a tendency towards the formation of leaves by the flattening and webbing of branch system and might have led to the development of large leaved vascular plants or the Pteropsida.

This line of evidence, therefore, suggests that the plants with microphyllous and megaphyllous leaves had separate lines of evolution. It suggests that the old division pteridophyta should be split up at least into two subdivisions, the Lycopsida and Pteropsida. The seed plants are included in the Pteropsida, along with the ferns, because they have megaphyllous leaves. The ferns are closer to the seed plants (spermatophyta) than to the Lycopsida and the Sphenopsida.

The above evidences lead us to conclude that the Psilophytales have originated from the green algae and have in turn given rise to the three subdivisions of the vascular plants, namely, the Lycopsida, Sphenopsida and the Pteropsida. It is also believed that the bryophyta have also originated from the green algae and have followed a different course of evolution that has ended blindly. It is also believed by some botanists that bryophytes may have originated as a result of retrogressive evolution accompanied by reduction, from the Psilophytales.

The Psilotales are regarded as the last living descendants of the Psilophytales. They have persisted through ages unchanged and have retained



in a remarkable manner their simple structure. The have been aptly regarded as the 'living fossils.'

Fuller and Tippo have drawn out a scheme (Fig. 3-13) of phylogenetic relationship among the various groups of vascular plants.

CHAPTER IV

LYCOPHYTA

Introduction

The division lycophyta is represented both by living and extinct genera and has a very long evolutionary history as it extends from the palaeozoic era [illegible] ...ted by [illegible] ...face of [illegible] ...eneral [illegible] This division is characterised by the following well defined features :—

1. The sporophyte shows clear distinction into stems, leaves and roots. 2. The stems and the roots branch freely in a dichotomous manner. In *Selaginella* the roots arise from rhizophores. 3. The leaves are *spirally* arranged and are microphyllous, *i.e.*, they are traversed only by a single unbranched vascular strand and the leaf traces do not leave a leaf gap. In some genera (*Selaginella* and *Isoetes*) the leaves are ligulate. 4. The vascular region may be [illegible] [illegible] produce exosporic gametophytes.

Classification

The division Lycophyta has been divided into two classes :

1. Class **Eligulopsida** which includes only one order :

(*a*) Order **Lycopodiales.** It comprises two families and have both *living and extinct plants.*

Family : **Lycopodiaceae.** It includes living as well as extinct plants : herbaceous, cambium absent, *sporophylls* with sporangia arranged in loose strobili; homosporous; exosporic gametophytes; sperms biflagellate. The family includes *Lycopodium, Phylloglossum* and *Lycopodites* (extinct).

Family : **Protolepedodendraceae.** *It includes the genus Protolepedodendron* which is extinct. It occurred in the Devonian age and had only primary growth; leaves forked; no definite strobili; gametophytes unknown.

2. Class **Ligulopsida.** It includes the following four orders :—

(*b*) Order **Selaginellales.** It includes both living and extinct forms. It is characterised by microphyllous and ligulate leaves which may be isophy-

llous or anisophyllous; strobili loose; heterosporous; gametophytes endosporic; secondary growth absent; spermatozoids biflagellate. It includes only one family **Selaginellaceae**. The family includes two genera, *Selaginella* (living) and *Selaginellites* (extinct).

(c) Order **Lepidodendrales.** Includes only extinct plants that had tree- [illegible] d ligulate leaves, [illegible] e of the genera [illegible] *Stigmaria*, *Sigi-* [illegible]

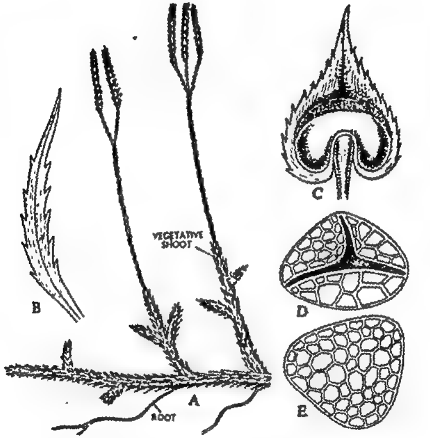


Fig. 4·1. Lycopodium clavatum. A. Portion of a plant showing habit; B. A sterile leaf; C. A sporophyll bearing sporangium; D. A spore seen from above showing triradiate ridge. E. spore showing reticulations of exine.

(d) Order **Isoetales.** Includes both living and extinct forms. They are characterised by sporophytes with a corm-like stem; perennial root producing meristem; secondary growth; small and ligulate leave; two types of spores; [illegible]

Heidelb. Akad. Wiss. 1959; Abh. 1, 2) (living) and *Isoetites* (extinct).

(e) Order **Pleuromeiales.** It is an extinct order with tree-like sporophytes that bore ligulate microphylls near their apices. They were heterosporous. It includes family **Pleuromeiaceae** with **Peluromeia** as one of the genera.

Class :— **ELIGULOPSIDA** Homosporous

Order :— **LYCOPODIALES**

The order is characterised by herbaceous and dichotomously branched stems, microphyllous leaves, absence of secondary growth, sporangia axillary or on adaxial side of the leaf, homosporous, exosporic, gametophytes, biflagellate sperms, protostelic or siphonostelic (*Phylloglossum*) stele; exarch or mesarch (*Phylloglossum*) xylem. The order includes the family *Lycopodiaceae* that includes two living genera, *Lycopodium* and *Phylloglossum*. The extinct genus *Lycopodites* flourished in the Carboniferous period. The life history of *Lycopodium* is discussed in this chapter.

LYCOPODIUM

Distribution and Occurrence

Lycopodium is a cosmopolitan genus with about 180 species that are found under varied habitats. Some of them grow in the colder climates of the arctic region. There are others that inhabit temperate, tropical and sub-tropical regions of the world. They are very common in the tropical zones. In India the genus is represented by thirty-three species (Chowdhry, 1937, Panigrahi, 1962). Most of them occur in the Eastern Himalayas and one in the Kumaon district. They are rare in the Western Himalayas. The stem is copi-

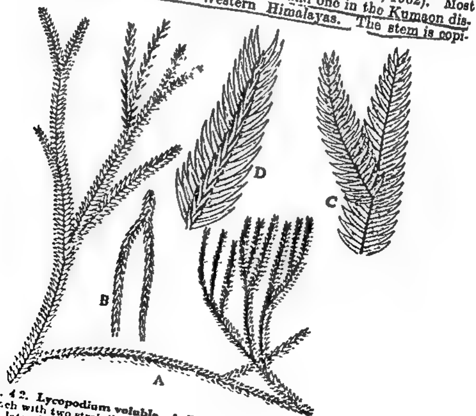


Fig. 4.2. Lycopodium volubile. A. Portion of a plant ; B. Fertile branch with two strobili ; C. Sterile branch with larger leaves in two lateral rows ; D. Portion of branch with two lateral rows of larger leaves and two rows of small leaves.

ously covered with sharp and pointed leaves. Their moss-like appearance and club-shaped strobili, earn them the name 'club mosses'.

Habit. Most of the tropical species are epiphytic and grow hanging from the tree trunks *L. phlegmaria* (Fig. 4·3), *L. squarrosum*. The temperate species grow in open wood-lands and on moist and acidic soils. *L. lucidulum* and *L. reflexum* are erect and shrubby forms. *L. clavatum*, *L. inundatum* (Fig. 4·1, 4·4) and *L. cernuum* are common creeping forms. *L. volubile* (Fig. 4·2) is a climber. The creeping forms give out erect branches at intervals.

Stem. The stem is dichotomously branched. The two branches formed as a result of dichotomy may be equal and continue to grow and undergo further dichotomy, or the two branches of a

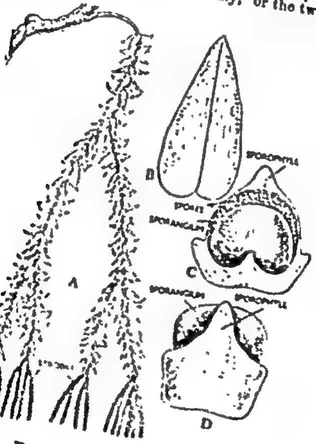


Fig. 4·3. *Lycopodium phlegmaria*.
A. The plant hanging from the host tree and showing pendent branches and strobili. B. a leaf; C–D. Sporangia with sporophylls.

dichotomy may be unequal, as one of them remains small and the other grows to a greater length. The smaller or the weaker branches may ultimately stop growth and bear strobili (Fig. 4·1). This type of branching (unequal dichotomy) is called pseudomonopodial

(*L. clavatum*). In prostrate species the main axis or the *rhizome* is completely or partially subterranean.

Leaf. The leaves are simple and small in size and posses a single median vein that fails to reach the leaf apex. Such leaves are called **microphyllous** or **microphylls.** The leaves lack a ligule. Usually the leaves are 2—10 mm. long but in some cases their [illegible] The leaves are spirally arranged and [illegible] in some cases the leaf arrangement may b[illegible] (*L. alpinum*) or even whorled (*L. verticillatum* and *L. cernuum*).

The leaves may be **isophyllous or anisophyllous** (*L. volubile*). The short branches in *L. volubile* bear four rows of leaves: two lateral rows of larger leaves, ventral row of smaller leaves, and a dorsal row of medium sized leaves. In addition to the normal leaves the trilbils in *L. selago* develop thick and fleshy leaves.

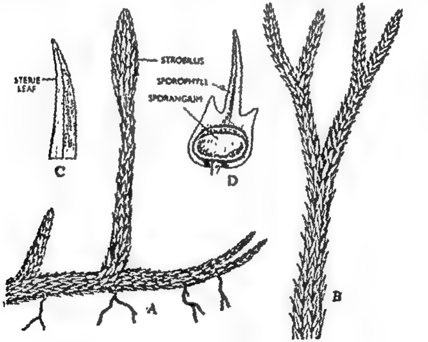


Fig. 4·4. *Lycopodium.* External morphology.
A. *L. inundatum.*
B. *L. selago*, note that the sporangia occur scattered and do not form a distinct strobilus.
C. A sterile leaf.
D. A sporophyll with sporangium.

Root. [illegible]

In the erect forms the roots come out from the basal part of stem. There are no roots elsewhere along the entire length of

the stem. In such cases the adventitious roots initiate near the shoot apex but do not come out of the stem, instead they grow downwards through the cortex and emerge out of the stem only near its base. A series of transverse sections of such stems show numerous roots in the cortex (Fig. 4·12). Such roots are called **cortical roots** and are found in *L. selago*, *L. pithyoides*, etc. Stockey (1907) reported as many as 52 cortical roots at one level of the stem in *L. pithyoides*. This is due to their acropetalous origin. The roots on coming out of the stem (aerial roots) branch freely in a dichotomous manner. In *L. clavatum* and *L. cernuum* (prostrate forms) the creeping axis bears adventitious roots all along its length. In these cases the root primordia take more direct course through the cortex.

Rothmaler (1944) suggested, on account of the variations in the genus, to split it up into four genera. He named these genera as *Lycopodium*, *Lepidotis*, *Diphasium*, and *Huperzia*. Rothmaler's treatment is also supported by the recent cytological investigations of the various species. His four genera show a complete cytological disparity. Pritzel (1900) divided the genus into two sub-genera which he named as *Rhopalostachya* and *Urostachya*. The former includes all those species that have prostrate main stems giving out erect secondary branches (*L. clavatum* and *L. cernum*). The latter includes the erect and epiphytic species (*L. pithyoides*, *L. selago*, *L. phlegmaria*, etc.). The *Urostachya* are regarded as primitive and show the following characters :—

1. They have erect or pendulous aerial axis.
2. The adventitious roots emerge out at the base.
3. Vegetative propagation by bulbils is common.
4. Lack of specialisation of the sporophylls.

The **Rhopalostachya** show the following features :—

1. The main stem is prostrate.
2. Bulbils rare.
3. Sporophylls specialised.
4. The roots may emerge at any point so that the whole axis is covered by adventitious roots.

Growth

The growth of the shoot takes place by means of an apical meristem which consists of a group of apical cells (Fig. 4·5). The derivatives of these cells differentiate into the primary meristematic tissue : the **protoderm**, the **ground meristem** and the **procambium**. The protoderm gives rise to the outer protective layer of the epidermis. The ground meristem differentiates the cortex, endodermis, pericycle and the pith. The procambium gives rise to the vascular tissue (xylem and the phloem). Wetmore (1943) has shown that the procambium is centrally located and extends very close to the shoot apex. Its cells are elongated and usually divide in a longitudinal plane and only frequently in transverse plane.

ANATOMY

Stem. A transverse section of the stem reveals :—

Epidermis. It is a single layer of parenchymatous cells with cutinised outer walls and stomata.

Cortex. It is present next to the epidermis and shows a great variation in its thickness and structure. Usually three types are recognisable :—

1. In some cases the whole of the cortex is made up of thin-walled cells. They enclose small or larger intercellular spaces. Such a cortex is called homogeneous (*L. selago*).

2. In some species the cortex in the mature stems is made up wholly of sclerenchymatous cells. There are no intercellular spaces between the cells.

3. In others (*L. clavatum*) the cortex is differentiated into three zones (Fig. 4·6, A).

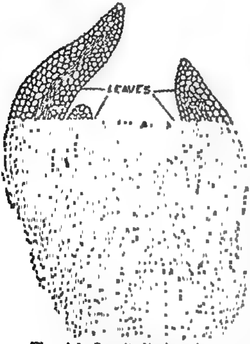


Fig. 4·5. Longitudinal section of stem-apex of Lycopodium reflexum. (After Hasupt)

(*i*) the outer zone of thick-walled cells (**Hypodermis**).

(*ii*) the middle zone of *large and thin-walled cells*. These cells enclose lot of intercellular spaces.

(*iii*) the inner zone of thick walled cells.

In *L. cernuum* the outer and inner cortex are thin-walled and the middle cortex is sclerenchymatous (*Fig.* 4·6, B).

The last layer of cortical cells is called the **endodermis.** Endodermis is clearly recognisable in the earlier stages *of development* because of the presence of casparian strips. As the development proceeds, in mature stems, the endodermal cells become thickened.

Pericycle. It is present next to the endodermis and is composed *of* one or many *layers of compactly* arranged parenchymatous cells.

Vascular Region or the Stele. It consists of only primary tissues, *i.e.,* the primary xylem and the primary phloem. The sporelings of all the species of *Lycopodium* show a central protostele with radiating arms, *i.e.,* actinostelic condition. When the sporelings grow the stelar structure goes on becoming complex and shows *variations* in various species. Sometimes the arrangement differs at different levels in the shoot of the same species. Basically the arrangement of primary xylem and phloem is a protostele. In this case *the* xylem forms the central core of the stem and pith is absent. The

phloem surrounds the xylem (Fig. 4·6, C). The protostele, as studied in the various species of *Lycopodium* shows variations with respect to its shape and arrangement of vascular tissues (xylem and phloem).

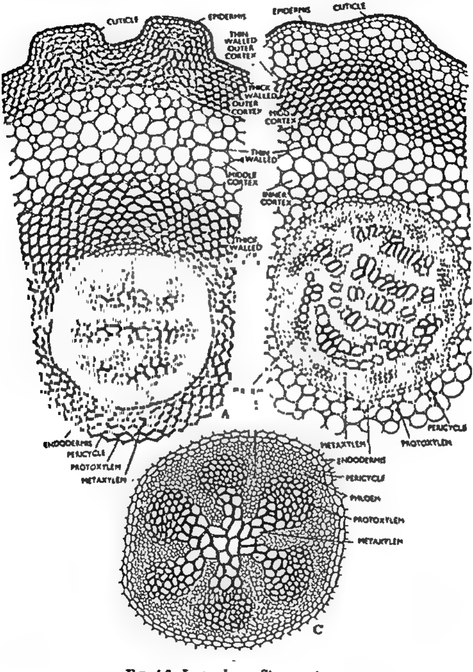


Fig. 4·6. *Lycopodium*—Stem anatomy.

A. *L. clavatum*—T. S. portion of stem. Note inner sclerenchymatous cortex.
B. *L. cernuum*—The middle cortex is sclerenchymatous.
C. *L. serratum*—Actinostelic protostele.

Generally it is sub-divided into four types : (*i*) **haplostele** in which the xylem forms a circular central core and the protoxylem may be in the centre or surrounding the metaxylem (absent in *Lycopodium*); (*ii*) **actinostele** (Fig. 4·6, C) in which the xylem appears star-shaped with protoxylem situated at the (Fig. 4·6, C) tips of the star-shaped projections and is exarch (*L. selago*, *L. serratum*, *L. phlegmaria*); (*iii*) **plectostele** in which the xylem, in a transverse section, appears to be in the form of separate plates of (*L. volubile*, *L. clavatum*) variable sizes with phloem in between them (Fig. 4·6) ; and (*iv*) **mixed protostele** in which the xylem and phloem are uniformly distributed and in a transverse section, it appears as if strands of xylem are embedded in the phloem (Fig. 4·8) which forms the ground mass (*L. cernuum*). The xylem is exarch.

In a plectostele the separate bands of xylem and phloem appear interconnected in a longitudinal section. They remain free only up to a certain distance up and below. In a mixed protostele the xylem occurs in the form of irregular tracheids scattered in the ground mass of phloem (Ogura, 1938). It is also found in *L. lateralis* and *L. drummondii*.

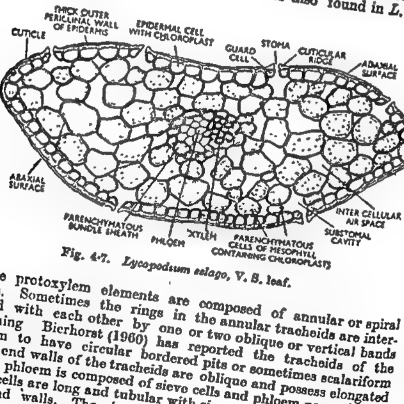


Fig. 4·7. *Lycopodium selago*, V. S. leaf.

The protoxylem elements are composed of annular or spiral tracheids. Sometimes the rings in the annular tracheids are interconnected with each other by one or two oblique or vertical bands of thickening Bierhorst (1960) has reported the tracheids of the metaxylem to have circular bordered pits or sometimes scalariform pits. The end walls of the tracheids are oblique and possess elongated pits. The phloem is composed of sieve cells and phloem parenchyma. The sieve cells are long and tubular with sieve areas on the lateral as well as end walls. The sieve elements develop centripetally from outer angles towards the centre.

Strands of vascular tissue called the **leaf traces** extend outwards from the stele and run obliquely upwards through the cortex. Only one strand enters the leaf to form a single median vein. Simi-

larly stele is connected with each branch by a **branch trace.** In a transverse section the leaf traces appear as distinct vascular strands. There are no leaf gaps.

Leaf :

The leaves are microphyllous and have a simple internal structure. In *Lycopodium clavatum* the leaf has a triangular outline in a transverse section. In *L. selago* (Fig. 4·7) the leaf is almost flattened. There is no distinct petiole and the leaf is transversed by a single midrib. A transverse section reveals the following structure :—

Epidermis. The epidermis is a single layer of compactly arranged cells sinuate and thick outer periclinal walls which are also covered by a layer of article. It is perforated by stomata which have only outer articular lodges. The cuticle extends over the guard cells. The stomata may be on both the sides of the leaf in isophyllous species and only on lower epidermis in some amosphyllous species (*L. volubile, L. complanatum*). It is so in *L. selago* (Fig. 4·7), which is isophyllous.

Mesophyll. It is undifferentiated and consists of loosely arranged chlorophyllose cells with small or large intercellular spaces. The cells may be round or oval or slightly lobed.

Vascular Region. A single unbranched vascular strand transverses the leaf. The vascular bundle is **mesarch.**

The xylem does not always show a clear distinction into proto- and metaxylem. Protoxylem when distinct is surrounded by metaxylem. Phloem is conspicuous only in the basal region of the leaf and surrounds the xylem. Near the apex of the leaf the vascular strand is composed by xylem alone. The tracheids in the xylem have spiral or annular thickenings. The phloem consists of sieve tubes and phloem parenchyma. The sieve tubes have narrow lumens. Endodermis or the bundle sheath may or may not be distinct.

Root (Fig. 4·8, A—C)

The adventitious roots arise from the pericycle (Roberts and Herty, 1934). A transverse section of the aerial root reveals the following structure :

Epidermis (Fig. 4·8, *A*). It consists of a single layer of thin-walled cells and is covered by numerous root hair. The root hair are arranged in pairs and their origin is characteristic for the genus *Lycopodium*. An epidermal cell divides either by an anticlinal or by an oblique wall into two daughter cells. These are called the **root hair initials.** Both of them give out root hair which therefore, lie in pairs. Epidermis is persistent in the aerial roots.

Cortex. In mature roots the cortex forms a broad zone and can be differentiated into two distinct regions. The outer cortex which is composed of several layers of thick-walled cells (Fig. 4·10) and the inner parenchymatous cortex. Endodermis and pericycle are not distinguishable.

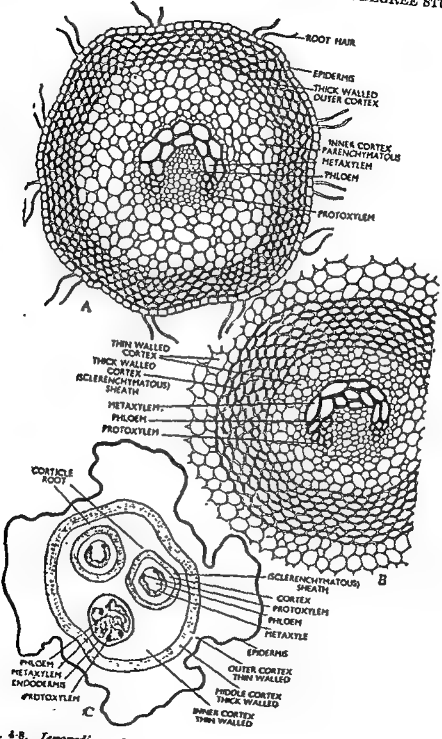


Fig. 4·8. *Lycopodium selago* : T.S. Root.
A. T.S. Aerial Root.
B. T.S. Cortical Root.
C. Diagrammatic T.S. through stem showing one stem stele and two cortical roots.

Stele. The stele may be diarch, tetrarch, or polyarch. In most of the prostrate or creeping species, *e.g.*, *L. clavatum*, the stele is polyarch. There is no pith and the stele consists, of six to ten plates of xylem arranged in a radial fashion. The xylem is exarch. The metaxylem of each radial plate of xylem unite in the centre to give a star-shaped appearance. The phloem is present in the form of patches in between the radiating arms of xylem. This structure is just like the actinostelic protostele.

In most of the erect and epiphytic species the stele is diarch or tetrarch. In *L. pithyoides* it is diarch and the xylem is crescent shaped with protoxylem at the end, *i.e.*, exarch. The phloem occupies the region between the two ends of the crescent shaped xylem (Fig. 4·8, A). There is only one group of phloem.

In *L. selago* the stele is diarch in one part of the root and tetrarch in the other. The diarch condition (Fig 4·10) is similar to the one described for *L. pithyoides* In tetrarch condition the stele reveals two separate bands of xylem with protoxylem at either end (exarch). The phloem lies between the xylem bands. This condition is somewhat similar to the plectostelic protostele.

The cortical roots (Fig 4·8, B and C) are almost similar in their internal organisation to the aerial roots. In the cortical roots the epidermis is not persistent and the root hair are absent or appear as small protuberances (trichoblasts).

The above account reveals a striking similarity in the internal organisation of the stem and the root The major differences being the absence of leaf traces and multicellular hair in the root. This similarity points towards a remarkable unity of the root and the shoot system. Such a similarity is seen only in the Lycopods because in the higher vascular plants there is a striking difference in the structure of the root and the stem. The striking similarity between the root and the stem morphology in the Lycopods points to their remote ancestry.

VEGETATIVE PROPAGATION

The sporophyte of *Lycopodium* reproduces vegetatively by the following methods :—

1. **By the Formation of Gemmae or Bulbils** (Fig 4·9, A—C) These are modified vegetative structures that arises as lateral outgrowths from near the stem apices and take the place of leaves. They have been reported in *L. selago*, *L. phlegmaria* and *L. lucidulum*. Each bulbil consists of a short and reduced axis surrounded by a number of thick and fleshy leaves. These leaves store food material. They remain on the plant till root primordia appear on the shortened stem. The gemmae fall on the ground near the parent plant and strike adventitious roots that penetrate the soil and establish the bulbil which later grows into a young plant (Fig. 4·14).

In *L. phlegmaria* bulbil-like structures have been reported to arise near the basal and older regions of the main stem (Chowdhry, 1933). Their germination or ultimate fate has not been reported but were considered to be organs of vegetative propagation.

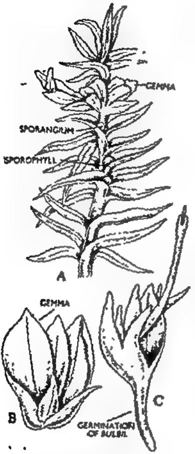


Fig. 4 9. *Lycopodium*. Vegetative reproduction.

A. Portion of stem of *L. lucidulum* bearing gemmae.

B A gemma

Morphology of the Bulbil

There has been a considerable discussion regarding the morphological nature of the bulbil. This has been regarded on purely morphological basis as being a modified sporangium, an arrested shank of a dichotomy, a lateral branch or a modified leaf. Its leaf-like nature is supported

show that if shoots of young plants are decapitated immediately below the apex, the young leaf rudiments transform into regenerative buds.

2. **Fragmentation.** Death and decay of older regions of the stem leading to the separation of younger branches which grow into separate plants is also a common method of vegetative propagation in *Lycopodium*.

buds of rhizome and its branches

vegetative propagation.

4. **Formation of Root Tubercles.** *In some species the adventitious roots bear swollen tubercles whose cells store food material. In L. ramulosum (Holloway, 1971), these tubercles originate from the parenchymatous region of the cortex. They consist of a group of cells with stored food material and protected by thick walls and have the capacity to germinate into new plants.*

5. Formation of Adventitious Buds. Such buds have been induced on isolated bulbil leaves. In the leaves epidermal cells proliferate near the base and grow into buds. Decapitation of stem near its apex also induces the formation of such buds. In this case the leaf rudiments change into such buds. In case decapitation is affected at lower levels such buds or regenerative outgrowths arise from the epidermis or from the stem cortex. They come out as adventitious buds. Such experiments of adventitious bud induction were carried out on *L. selago* by Willams (1933) Goebel reported the formation of such buds from isolated leaves of sporelings in *L. inundatum*. These buds are capable of germinating into new plants.

ORGANISATION OF THE STROBILUS

In the simple and primitive species of *Lycopodium* all of which belong to the *Urostachya L. selago, L lucidulum, L. squarrosum*, etc., every leaf on the plant is a sporophyll or at least potentially so. In the species belonging to *Rhopalostachya* and in some species belonging to *Urostachya* (*L phlegmaria*), the leaves near the apices of the branches bear sporangia and are called the **sporophylls**. The lower leaves in these species are sterile and function merely as foliage leaves. Aggregation of sporophylls is called the **strobilus** or the **cone**. The arrangement of the sporophylls may be loose when they form a lax or a loose **strobilus** or they may be arranged compactly to form a compact or a definite **strobilus**. The compact type of strobilus is a stem with short internodes bearing sporophylls. It develops from an apical meristem and its vasculature is similar to that of vegetative axis.

In *L. selago* and *L. reflexum* (Fig. 4·4, *B*) the sporophylls are similar to the foliage leaves and are arranged in a loose manner at intervals all along the erect branches. Such an arrangement gives rise to the alternating fertile and sterile regions. Such a condition is regarded by many morphologists as a strobilus comprising the entire plant. The supporters of this view regard the foliage leaves as secondarily sterilised sporophylls. Such a conclusion is based on the observation that such leaves also bear abortive sporangia. The same is the condition in *L. lucidulum*. In *L. squarrosum* the strobilus is terminal in position but can be hardly distinguished from the sterile region because the sporophylls are similar to the foliage leaves and are loosely arranged.

In *L. phlegmaria* (Fig. 4·3) the sporophylls are smaller than the foliage leaves and are arranged in a compact manner to form distinct strobili (Fig. 4 3) at the distal ends of the stem and its branches. The strobili in this species are dichotomously branched and pendulus.

In the section *Rhopalostachya* there is a great variation among the sterile leaves and the sporophylls. In *Lycopodium inundatum* (Fig. 4·4, A) the sporophylls differ only slightly from the sterile leaves and the strobilus is not very distinctly marked off from the

vegetative shoot. The sporophylls are slightly modified (Fig. 4·4, D) so as to protect the sporangium.

In *Lycopodium annolinum* the strobilus is quite distinct from the vegetative shoot. The sporophylls are quite distinct from the sterile or vegetative leaves. Each sporophyll has an abaxial outgrowth or a flange that protects the sporangia belonging to the lower sporophylls. The strobili of this species terminate normal leafy branches and the sterile leaves are all alike.

In *L clavatum* (Fig. 4·1) the strobili are quite distinct and compact and are borne at the tips of special erect shoot, *i.e.*, they are not borne by all the erect branches. The branches bearing strobili have vegetative leaves that are small and scale-like. They are yellowish green in colour. The leaves of sterile branches are comparatively large and green in colour. So in this case the sterile leaves are of two kinds.

In *L. volubile* (Fig. 4·2, A—D) there are three or four kinds of sterile leaves. The creeping axis in this species bears long and needle shaped leaves. The branches bear four rows of leaves. Of these the two lateral rows have broad falcate leaves, the lower row has hair-like leaves and the dorsal row has medium-sized needle-like leaves. The strobili terminate younger branches that arise on the younger parts of the axis The strobili are compact and branched (Fig. 4·2, B). The sporophylls posses a small bulge or a flange on the ventral (abaxial) side. This outgrowth affords some protection to the sporangia below.

Apart from the variations in the shape and the size of the sporophylls there is also a considerable variation regarding the position of the sporangium with respect to the sporophylls. In *L. selag* (Fig. 4·4, B), *L. lucidulum* (Fig. 4·9, A), and *L. inundatum* the spor angia are axillary in position (Fig. 4·4, A). In *L. cernuum* anc *L. calvatum* (Fig. 4·10,A) the sporangium arises on the dorsal (adaxial) surface of the sporophylls, that is, it is **'foliar'** or **'epiphyllous'**. In *L. squarrosum* the position is sub-foliar, that is, in this case the sporangium does not arise exactly in the axil of the sporophyll, but a little towards the sporophyll. Every sporophyll is supplied from the stele of the stem by a single trace.

A careful perusal of the facts cited above give us a clear picture of the variations among the species of *Lycopodium*. With these facts available to us, it is not difficult to arrange a series representing progressive stages in the differentiation of the sporophylls and organisation of a strobilus. Such a series is a clear manifestation of a course of evolution that the more complex species have followed. In the simpler species where there is no or very little differentiation between vegetative and reproductive regions the stems are dichotomously branched and possess a radial type of stele. The cone bearing species on the other hand have stems with monopodial branching and most of them show the parallel-banded type of stele. (Plectostele).

SPORANGIUM

The position of the sporangium with respect to the sporophyll has already been discussed. Regarding its shape the sporangium is

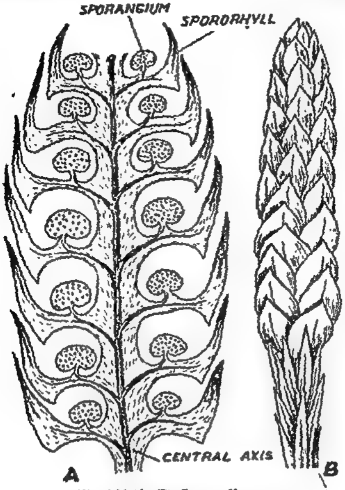


Fig. 4.10 (A—B). Lycopodium.
A. V.S. portion of strobilus of *L. clavatum*.
B. A compact strobilus of *L. stichense*.

mostly reniform or kidney-shaped (Fig. 4.1, C; 4·2, C, D; 4·10) and sometimes sub-spherical and varies in diameter [illegible] mm. It is usually [illegible] *L. cernuum*, *L. clavatum*, [illegible] In the latter case they are protected by flange like outgrowth from the sporophylls above. They vary in colour from orange to yellow and are unilocular.

Structure of the sporangium

A longitudinal section of a fully developed sporangium of all he species of *Lycopodium* presents an almost identical internal set-up

(Fig 4·11, G). There are minor differences regarding the length of stalk number of wall layers and amount of sporogenus tissue. Every sporangium is clearly distinguishable into two (Fig. 4·11, F, G) prominent parts (*i*) the **stalk** and (*ii*) the **capsule**.

The stalk may be short or may be just represented by a cushion of cells. It may be narrow as in *L. selago* or broad as in *L. alpinum*.

The stalk bears a curved and reniform capsule which is not lobed a [illegible] 4·10, A). It has a three or mor[illegible]s of spore mother cells (Fig. 4·1[illegible] wall is three layered at the apex and may be more than three layers near its base. The innermost layer of wall is called the *tapetum*. The tapetum forms a complete investment of t[illegible] cells are prominent due to the more [illegible]asm and bigger nuclei. These cells [illegible] tapetal layer maintains its identi[illegible]rangium [illegible]us cells separate and round [illegible]11, G) which undergo tetrad [illegible] tetrads are tetrahedral and after secreting their own walls they separate into spores. The number of spores per sporangium varies considerably.

Development of the Sporangium (*Fig. 4·11, A—G*)

The development of the sporangium in the genus *Lycopodium* was studied in detail by Bower (1894). The development in *L. selago* in given below :—

[illegible] from a single transverse [illegible] surface [illegible]chment [illegible] row is visible and it appears as if the sporangium develops from a single cell. As a matter of fact all the cells in this transverse row take part in the development of the sporangium. Each of these cells divide periclinally to form a middle row of **archesporial cells** (Fig. 4·11, [illegible]

[illegible]

lower cells as they appear in a tangential section constitute the **sub-archesporial cells.** Since the sporangium originates from a group of cells the development is of the **eusporangiate** type.

The primary wall cells undergo periclinal and anticlinal divisions to form a three or more layered thick sporangial walls. The inner[illegible] layer of wall is differentiated as the **tapetum**. Its cells are [illegible] contain stored food material. This layer provides

(Fig 4·11, G). There are minor differences regarding the length of stalk number of wall layers and amount of sporogenus tissue. Every sporangium is clearly distinguishable into two (*Fig.* 4·11, *F, G*) prominent parts (*i*) the **stalk** and (*ii*) the **capsule.**

The stalk may be short or may be just represented by a cushion of cells. It may be narrow as in *L. selago* or broad as in *L. alpinum.*

The stalk bears a curved and reniform capsule which is not lobed and is unseptate and unilocular (Fig. 4·10, A). It has a three or more layered wall surrounding a mass of spore mother cells (Fig. 4·11, G). In *L. selago* the sporangial wall is three layered at the apex and may be more than three layers near its base. The innermost layer of wall is called the *tapetum*. The tapetum forms a complete investment of the sporogenous tissue. Its cells are prominent due to the more granular nature of their cytoplasm and bigger nuclei. These cells contain nutritive substance. The tapetal layer maintains its *identity* throughout the *life* of the sporangium and never disintegrates. The sporogenous cells separate and round off to form **spore mother cells** (Fig. 4 11, G) which undergo tetrad formation as a result of meiosis. The tetrads are tetrahedral and after secreting their own walls they separate into spores. The number of spores per sporangium varies considerably.

Development of the Sporangium (*Fig.* 4·11, *A—G*)

The development of the sporangium in the genus *Lycopodium* was studied in detail by Bower (1894). The development in *L. selago* in given below :—

T[illegible] nates from a single transverse [illegible] on the dorsal or upper surface [illegible] e to its point of attachment [illegible] ly one of the cells in a row is visible and it appears as if the sporangium develops from a single cell. As a matter of fact all the cells in this transverse row take part in the development of the sporangium. Each of these cells divide [illegible] archesporial cells (Fig 4·11, [illegible] primary wall cells [illegible] tapetum [illegible] lower cells as they appear in a tangential section constitute the **sub-archesporial cells.** Since the sporangium originates from a group of cells the development is of the eusporangiate type.

The primary wall cells undergo periclinal and anticlinal divisions to form a three or more layered thick sporangial walls. The inner[illegible] of wall is differentiated as the **tapetum.** Its cells are [illegible] contain stored food material. This layer provides

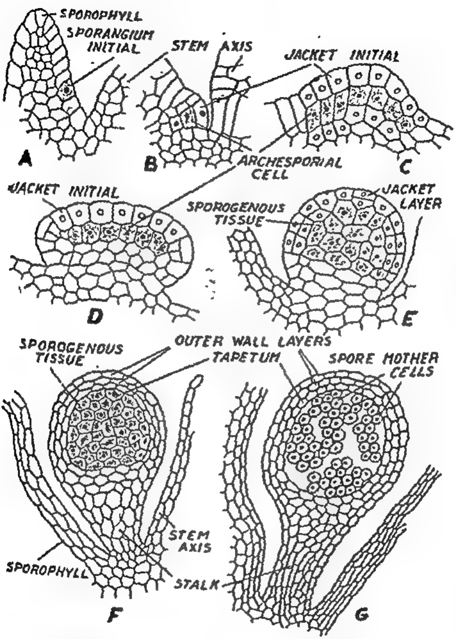


Fig. 4·11 (A—G). Lycopodium selago. Various stages in the development of sporangium.

A, B. Radial sections through ... Shows sporangial ... periclinally into a ...

C.

D.

E.

F. ... g two-wall layers, ...tum, and sporogenous tissue.

G. A later stage showing spore mother cells (All after Bower).

Structure of the Spore

Lycopodium is homosporous. The spores are unicellular and range in diameter between 0·03—0·05 mm. The spores occur in tetrahedral tetrads and hence have a tetrahedral shape with a rounded or semicircular base (Fig. 4·1, D, E). Each spore has a triradiate ridge and is enclosed within a thin or thick spore wall. The spore wall has two layers (Afzelius *et el*, 1954). The inner layer as revealed by ultramicroscope studies is granular and is surrounded by an outer layer which is made up of concentric lamellae. Each spore has a single haploid nucleus surrounded by cytoplasm which is filled with reserve food material (fats and oils). The chloroplasts may or may not be present.

The spore wall may be smooth or it may be variously sculptured (Fig. 4·1, D, E). Sculpturing may be in the form of pits or reticulate ridges as in *L. complanatum*, *L. clavatum* (Fig. 4·1, D, E.) In *L. selago* and *L. phlegmaria* the outer spore wall is beset with rounded or peg-like outgrowths. In *L. inundatum*, *L cernum* and some other species the outer layer of the spore wall is thrown into slightly raised ridges that alternate with shallow grooves. In some species of *Lycopodium* the spore wall is thick and cutinised.

Germination of the Spore (Fig. 4·12, A—F)

The time taken by the spores to germinate varies from a few days after their liberation from the sporangium to several years (3 to 8 years). This unusual delay in germination of spores has been attributed, by some workers (Bruchmann; Barrows, 1935) to their thick and cutinised walls. In case the spores germinate within a few days of their liberation from the sporangium, they produce aerial short lived and green prothalli, *e.g.*, *L. cernuum* and *L. inundatum*. In case the spores take a longer time to germinate, they get buried under the soil and produce colourless and subterranean prothalli that are comparatively large and tuberous and long-lived, *e.g.*, *L. clavatum*, *L. complanatum*, *L. obscurum* and *L. annotinum*.

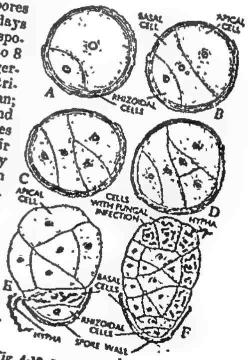


Fig. 4·12. Lycopodium annotinum. Various stages in the germination of the spore. (After Bruchmann)

There is great variation in the genus regarding the details of spore germination. The usual steps that lead the spore to the formation of mature prothallus are outlined below ;

cells. The tapetal layer in *Lycopodium* remains intact and does not undergo disorganisation to form the **periplasmodial** fluid.

The **archesporial cells** whose number is not constant, although it is seven in most of the developing sporangia of *L. selago* divide in various planes to form a group of cells called the **sporogenous tissue**. These cells then grow in size, round off and separate from one another to form **spore mother cell or sporocytes**. The sporocytes undergo meiosis and produce **tetrahedral tetrads** of haploid spores. These finally separate and secrete a wall whose ornamentation varies with species. The fully grown sporangium is more of less reniform and possess a short stalk.

Lycopodium selago shows the type of sporangial development that can be regarded as characteristic for the section *Urostachya*. The other species of this section that were studied by Bower included *L. dichotomum*, *L. carinatum*, *L. nummularifolium* and *L phlegmaria*. The unique feature that is common in all of them is the development from a single row of initials, of a single tangential row of **archesporial cells**. There are, however, differences in the number of cells in the archesporial row and in the number of layers in the sporangial wall. In *L. dichotomum* the sporangial wall is 4–7 layers thick.

In *L inundatum* which belong to *Rhopalostachya* there are two tangential rows of archesporial cells as compared to one in *L. selago*.

However in *L. clavatum*, and *L. alpinum*, both of which belong to *Rhopalostachya* group there are three tangential rows of archesporial cells. The sporangium thus is more massive. In these species the **subarchesporial** pad is comparatively well developed and extends in between the sporogenous tissue as small processes. The sporangial stalk is thick and short as compared to the long and narrow stalk in *L. selago*. Bower regarded *L. inundatum* as an intermediate form linking the two types of sporangial development in *L. selago* and *L. clavatum*.

Dehiscence of Sporangium

In species which compact strobili the dehiscence of the sporangium is preceded by elongation of the internodes of the central axis. As a result the sporophylls spread out and expose the sporangia. The sporangia dehisce along a line of cells running across the upper surface of the kidney-shaped sporangium. This line of cells is differentiated in the outermost layer of sporangial wall and may be designated as the **stomium**. The inner walls of the cells constituting the stomium are thick and lignified. The cells making up the bulk of sporangial wall, other than the stomium, have their side walls thickened only. As the exposed sporangia lose water and dry, a condition of stress and strain develops in the cells of the sporangial wall. These stresses lead to the appearance of a slit in the stomium and cause the sporangial wall to split open from top to the base of the sporangium in the form of two valves. The loose spore mass projects out of the open slit. The air currents scatter the spores and disseminate them.

GAMETOPHYTE

It starts with the spore that germinates to give rise to a new individual called the **gametophyte or the prothallus**.

Structure of the Spore

Lycopodium is homosporous. The spores are unicellular and range in diameter between 0·03—0·05 mm. The spores occur in tetrahedral tetrads and hence have a tetrahedral shape with a rounded or semicircular base (Fig. 4·1, D, E). Each spore has a triradiate ridge and is enclosed within a thin or thick spore wall. The spore wall has two layers (Afzelius *et el*, 1954) The inner layer as revealed by ultramicroscope studies is granular and is surrounded by an outer layer which is made up of concentric lamellae. Each spore has a single haploid nucleus surrounded by cytoplasm which is filled with reserve food material (fats and oils). The chloroplasts may or may not be present.

The spore wall may be smooth or it may be variously sculptured (Fig. 4·1, D, E). Sculpturing may be in the form of pits or reticulate ridges as in *L. complanatum*, *L. clavatum* (Fig. 4·1, D, E.) In *L. selago* and *L. phlegmaria* the outer spore wall is beset with rounded or peg-like outgrowths. In *L. inundatum*, *L. cernum* and some other species the outer layer of the spore wall is thrown into slightly raised ridges that alternate with shallow grooves. In some species of *Lycopodium* the spore wall is thick and cutinised.

Germination of the Spore (Fig. 4·12, A—F)

The time taken by the spores to germinate varies from a few days after their liberation from the sporangium to several years (3 to 8 years). This unusual delay in germination of spores has been attributed, by some workers (Bruchmann; Barrows, 1935) to their thick and cutinised walls. In case the spores germinate within a few days of their liberation from the sporangium, they produce aerial short lived and green prothalli. *e.g.*, *L. cernuum* and *L. inundatum*. In case the spores take a longer time to germinate, they get buried under the soil and produce colourless and subterranean prothalli that are comparatively large and tuberous and long-lived, *e.g.*, *L. clavatum*, *L. complanatum*, *L. obscurum* and *L. annotinum*.

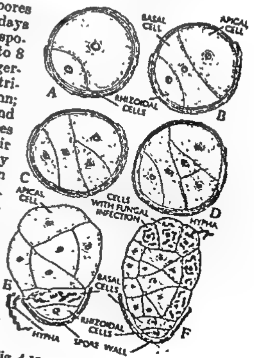


Fig. 4·12. Lycopodium annotinum. Various stages in the germination of the spore. (After Bruchmann)

There is great variation in the genus regarding the details of spore germination. The usual steps that lead the spore to the formation of mature prothallus are outlined below ;

The spores germinate under moist conditions. They absorb [illegible] the spore wall ruptures along the tri- [illegible] of the spore have already divided into two unequal cells. One of these cells is small and lenticular or bicon-

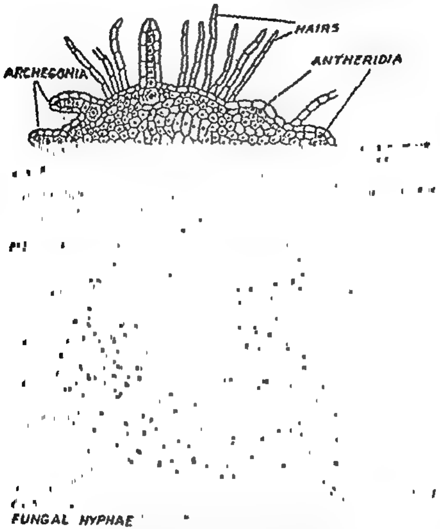


Fig. 4·13. Lycopodium selago.
A mature prothallus showing details of internal structure. The generative region bears antheridia and archegonia
(After Bruchmann)

vex and lies under one of the three arms of the triradiate mark. The rest of the spore is occup [illegible] called the rhizoidal cell and [illegible] of [illegible] up- [illegible] cts [illegible] ll. It soon divides [illegible] cells. The second [illegible] lls differentiates the

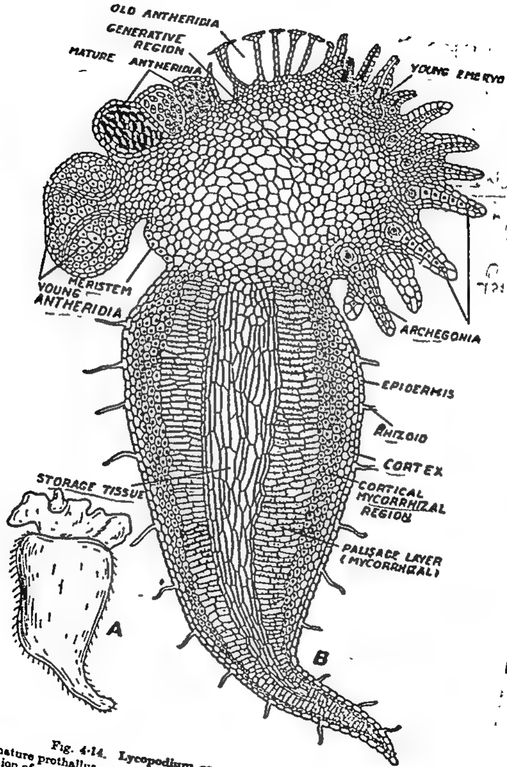


Fig. 4·14. Lycopodium complanatum.

A. A mature prothallus.
B. Section of a mature prothallus showing details of internal structure (After Bruchmann).

basal cell lying next to the **rhizoidal cell** and the third cell (Fig. 4·12). At this stage the young. Prothallus has three cells. These are the **rhizoidal cell**, the **basal cell** and the **upper cell**.

The third cell divides further by two successive divisions to differentiate an **apical cell with two cutting** faces (Fig. 4·12, E). This is the five-celled stage of the young prothallus. At this stage the cells are devoid of chl... In the species destir ... of the stages leadin ... npleted within the s ... attack of the mycorrhizal fungus. In case the ... the five-celled prothallium ... ung prothallus may die. ... urther growth stops at tl ... about a year intervenes ... During this interval th ... infection takes place (*Fig.* 4·12, *E, F*). This infection takes place through the basal cell (Fig. 4·14, D) and it is believed that physiologically, the fungus supplies certain substances vital for the proper development of the prothallus. Further growth is resumed and is marked by the activity of the apical cell which cuts off six segments. Later the apical cell is replaced by a group of meristematic cells. These cells divide repeatedly and contribute to the further development of the prothallus.

Wetmore and Morel (1951) cultivated the spores of *L. cernuum* in cultu... ...inerals and glucose. The spores first divide into two unequal cells. The large divides by oblique walls to cut ... cuts off segments to form a mass of ... the **primary tubercle** (Treub, 1884). Further development is arrested here and continues further only if an endophytic fungus attacks the cells. Resumption of further growth results in the characteristic shape of the prothallus of *L. cernuum*. It takes six months under controlled conditions.

Structure of Mature Prothallus

The structure of the mature prothallus, in various species of *Lycopodium*, was described by Treub (1884, 1889) and Bruchmann (1898—1916). As a result of their studies three inter grading types of prothalli (Figs. 4·14, 4·15, 4·25, 4·26) have been discovered. These are : (i) Green and aerial prothalli with a lower conical sub terranean region and upper epiterranean green and lobed portion. The latter bears photosynthetic lobes among whose bases the sex organs are produced. *L. cernuum* (Fig. 4 27), *L. inundatum* and *L. salakense* exemplify this type of prothallus ; (*ii*) completely subterranean or underground prothalli that are fleshy, non-green and totally saprophytic. They lack photosynthetic lobes and the sex organs are borne on the upper surface of the prothallus, *e.g.*, *L. annotinum*, *L. complanatum* (Fig. 4·14), *L. obscurum*, and *L. clavatum* (Figs. 4·15 and 4·25) ; (*iii*)

this is typified by *L. phlegmaria* (Fig. 4·25) and consist of cylindrical, branching and nongreen prothalli whose elongate branches may become independent as a result of apical growth and posterior decay. These three types will be discussed in detail.

First Type

It is exemplified by *L. cernuum* and *L. inundatum*. The prothallus in *L. cernuum* (Fig. 4·26, A—E) has an erect cylindrical body only two to three millimetres long. It grows at the surface of the ground and consists of a colourless basal portion buried in the soil and a conspicuously lobed aerial crown that is green and bears sex organs at the bases of the green lobes. The rhizoids are restricted to the lower buried portion which also contains an endophytic fungus.

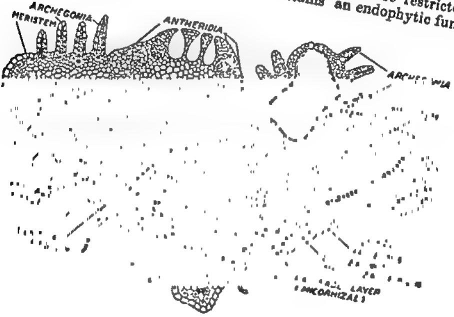


Fig. 4·15. *Lycopodium clavatum*.
Section through the prothallus showing detailed internal structure.
(After Bruchmann)

This prothallus is independent because it manufactures its own food. The prothallus of this species reaches maturity within six months and grows by means of a meristematic zone that is present below the apex and is marginal in position. It forms a rim around the cylindrical upper part of the prothallus. The sex. organs develop from cells cut off by the meristem and the youngest is present near the meristem. The portion of prothallus bearing the sex organs is called the **generative zone.** This zone is green and is made up of undifferentiated parenchymatous cells, which are devoid of fungal hyphae. In *L. salakense* the green lobes rudimentary or even absent. This species lacks endopytic fungus.

Second Type

This type includes subterranean prothalli that have acquired a saprophytic mode of nutrition. It is represented by *L. complanatum* (Fig. 4·14), *L. clavatum* (Figs. 4·15 and 4·16), *L. annotinum* and *L. obscurum*. The prothalli in all these species are tuberous, yellowish brown or even colourless. They store sufficient food material and vary in dimensions from 12 to 18 mm. long. Their shape also varies and may be top-shaped (*L. clavatum*), carrot-shaped or conical (*L. complanatum*) and discoid. They have ... distinct regions (i) the lower ... the upper [illegible]

[illegible] numerous ... the several layered **cortical** ... which is composed of tightly packed *parenchymatous cells that are* filled with the endophytic fungal hyphae. Next to this zone is the **palisade zone** which is made up of closely packed columnar cells that also contain hyphae (Fig 4·14). Next to this is the **central storage zone** *whose cells are* filled with stored food (Fig. 4·14). The upper broad region of the prothallus is called the **generative region** and is a broad expanse of parenchyma cells unaffected by ... the fungus. It has a margi- [illegible] ...d 4·16) and bears sex organs on [illegible] ...nia are found near the margins and the antheridia are ... [illegible] ...lly. In *L. complanatum* (Fig. 4·14), the upper broad region is irregularly lobed and bears sex organs. The lobes in this case are not as prominent as in the aerial prothalli of *L. cernuum*. In *L. Clavatum* the lobes are absent and the upper generative region is flat and irregularly cup-shaped (Fig. 4·15) with a depressed centre surrounded by a broad rim. In *L. obscurum* De Maggio (1967) induced the formation of tracheids in the prothallus. Under cultural conditions the prothalli were exogenously supplied with various concentrations of sucrose, cytokinins, gibberilins and auxins singly and in combination. Quantitative analysis revealed that sucrose alone is an efficient substrate for tracheid induction.

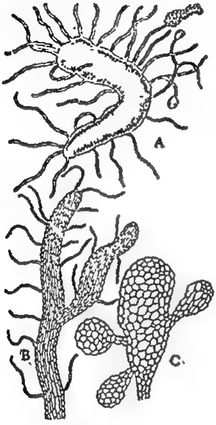


Fig. 4·16. Lycopodium phlegmaria. A. Mature prothallus covered with numerous filamentous outgrowths. B. A sterile prothallus. C. A gemma bearing secondary gemmae. (After Goebel)

Third Type

This type includes colourless, subterranean, saprophytic and

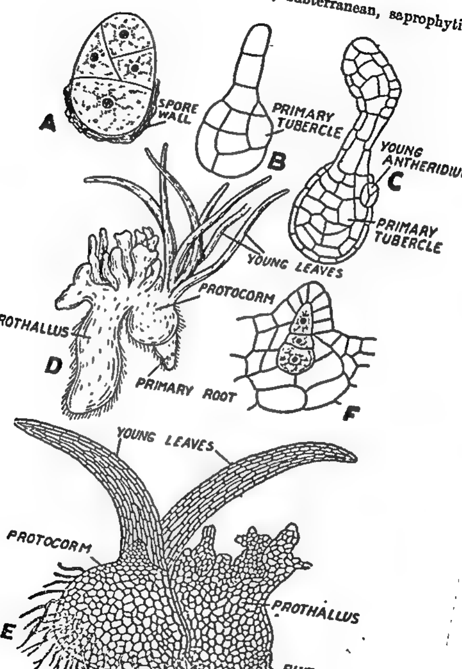


Fig. 4·17 (A—F). Lycopodium cernuum. Gametophytic generation.
A. B. Younger stages of development.
C. An older stage with the first antheridium.
D. A mature prothallus with attached young sporophyte.
E. The same as D.
F. A mature archegonium. (After Treub)

repeatedly branched monopodial prothalli that are found only in the epiphytic species of *Lycopodium*. The typical type is represented by *L. phlegmaria* (Fig. 4·16, A—C). The prothallus bears colourless and cylindrical branches and grows in the humus collected on the branches of the trees on which this species grows. The branches arise irregularly and ramify into the dead bark. The prothallus is attached to the substratum by means of absorbent rhizoids that grow in all directions. The growth of the prothallus and its branches is apical and takes place by the activity of two prismatic initial cells that lie side by side. The divisions of these cells do not follow a regular sequence and are irregular. In this case the endophytic fungus is found in the inner core of cells. These cells also store oil as reserve food. This centrally located mycorrhizal region is surrounded by one or more layers of cortical cells that are devoid of endophytic fungus and are colourless. The rhizoids arise from the outermost layer. The prothallus is marked by unlimited apical growth followed by progressive death and decay of older regions. This leads to fragmentation and thereby to vegetative propagation of the prothallus. The branches also bear, near their apices, shortly stalked and multicellular bodies called the **gemmae** (Fig. 4·16, C). They get easily detached and can germinate to produce new prothalli. The sex organs are borne on the upper surface of the branches and are always intermingled with paraphyses. The branches bear both antheridia and archegonia but antheridia always develop first.

The prothallus in *L. selago* (Bruchmann, 1910) may be subterranean or epiterranean (aerial). In case the spores of this species germinate soon after their liberation and are not buried under the soil, they give rise to an aerial and photosynthetic prothallus. If the spores are buried under the soil they give rise to a pale and a subterranean prothallus. Regarding the form of the underground prothallus, it depends upon the depth and character of the soil. If the soil is firm, the prothallus is elongated and cylindrical in form. In an open and loose soil the prothalli are compressed and flattened and taper below into a conical point (Fig. 4·13). The upper region is broad and cup-shaped and bears sex organs. It is also called the [illegible] fungus. It is lobed and the [illegible] inwards. The outer side [illegible] eble transition to dorsiventrality. The meristematic zone occupies the margin of the cup-[illegible] region. The [illegible] outer layer [illegible] g endophytic [illegible] halli of *other* [illegible] orsiventrality [illegible] within the genus and elsewhere. The antheridia are borne in a regular sequence from the centre to the marginal meristem (Fig. 4·18) and are followed by archegonia (Fig. 4·19). The lobes bearing the sex organs also bear paraphyses. The underground prothalli of *L. selago* when growing near the surface of the soil may emerge out partly and become green in colour. Such prothalli are partly colourless and partly green. *So*

we derive the following conclusions from the study of the prothallus of *L. selago.*

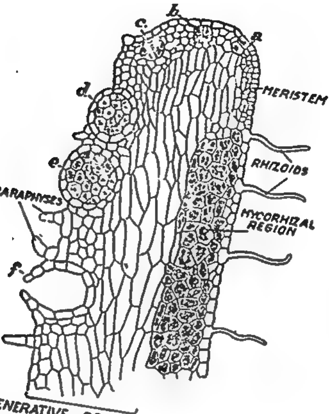


Fig. 4·18. **Lycopodium selago.** A median longitudinal section through the antheridia bearing region of prothallus showing antheridia in various stages of development (a—f). (After Bruchmann).

1. They are green and photosynthetic when aerial.

2. They may be partly green and partly colourless or they can be partly subterranean and partly epiterranean.

3. Their form may be obconical below and flat and lobed above as in prothalli growing in loose soil.

4. They assume a cylindrical form in firm soil or when growing in rotten wood they give out branches that show a dorsiventral symmetry.

5. They exhibit both holophytic and saprophytic nutrition.

6. The aerial region of the thallus is lobed.

The subterranean gametophytes of *L. selago* resemble the gametophytes of epiphytic species like *L. phlegmaria* (Treub 1884-1890) and *L. billardieri* (Holloway, 1916-1920) in possessing slender and cylindrical branches and in the presence of paraphyses among the sex organs. The underground prothallus of *L. volubile*

which is very much like that of *L. clavatum* resembles *L. selago* in that it sometimes emerges out of the soil and develops chlorophyll.

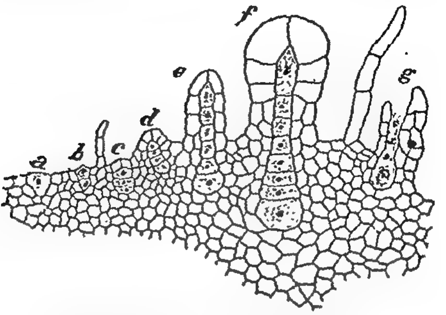


Fig. 4·19. Lycopodium selago. L.S. through archegonial region of the prothallus showing archegonia in various stages of development (a—g). (After Bruchmann.)

L. clavatum, L. complanatum, L. annotinum, L. volubile and other subterranean species have at least of a few common stages in their ontogeny with that of *L. selago*. These are—(*i*) the presence of a two sided apical cell in the earlier stages of development; (*ii*) further development depending upon the attack of endophytic fungus; (*iii*) formation of a meristematic zone whose position is marginal; (*iv*) the obconical or conical shape of the lower region; and (*v*) presence of lobes in the upper region. The prothalli of all these subterranean species resemble with that of *L. selago* in their saprophytic mode of nutrition.

The aerial prothalli of *L. cernuum*, *L. inundatum* and *L. salakense* resemble that of aerial prothalli of *L. selago* in several respects. The common features being:

(*i*) Their autophytic mode of nutrition.

(*ii*) Their green colour.

(*iii*) Presence of lobes in the upper distal region

(*iv*) Rhizoids restricted only to the lower conical region.

(*v*) The mycorrhiza also restricted to the lower conical portion and is distributed in much the same manner.

(*vi*) Presence of sex organs in the upper lobed region

(*vii*) Earlier stages of development and presence of meristem

It becomes clear from the above account that prothallus of *L. selago* bears resemblances to all the three types of prothalli of *Lycopodium*. It can, therefore, be regarded as an intermediate type which links together the three types of prothalli. Partly subterranean and partly epiterranean types of prothalli of *L. selago* and *L. volubile* are, in a sense, intermediate between the authophytic and saprophytic types. Such a link has been pointed out by Lang (1899), Campbell (1939), and Bower (1935). Manton (1950) studied the cytology of four British species of *Lycopodium* and as a result she came to the conclusion that *L. setlago*, often considered to be a central and primitive type, is found on cytological evidence, to be a hybrid of very high chromosome number.

As a matter of fact the grouping of the gametophytes of various species of *Lycopodium* into three types is only superficial and is based on differences in the form and appearance of the mature prothalli.

Vegetative propagation of the prothallus

The prothallus in some species of *Lycopodium* reproduces vegetatively by the following methods :

1. **By the formation of gemmae**. They are borne on the branches of the prothallus in *L. phlegmaria* and arise singly or in clusters near the tips of the branches. Each gemma (Fig. 4·25 C) on separation from the parent prothallus grows into a new prothallus. A gemma develops from a single superficial cell of the branch and is usually a large club-shaped and shortly stalked structure. In starved prothalli the gemmae are few celled and thick walled and their cells store food material. They are capable of perennating and germinate into new prothalli on the advent of favourable weather.

2. By the progressive decay of the older parts of the prothallus and thereby separating the younger branches, which behave as individual prothalli. This method is very common with the gametophytes of *L. phlegmaria* and *L. billardieri*.

3. In *L. inundatum* vegetative buds or gemmae arise from the injured parts of the lobes.

Sex Organs

The exosporic gametophytes of *Lycopodium* are essentially monoecious but protandrous. The antheridia and archegonia, in most of the species of *Lycopodium*, are formed in distinct patches or clusters on the upper surface of the prothallus. In *L. lucidulum* Spessard (1922) reported intermingling of the antheridia and archegonia. There is a remarkable similarity in early development and initiation of sex organs in the genus. Both the antheridia and the archegonia develop from a surface cell called the **initial cell.** In both, this cell divides first by a periclinal wall which separates the sterile **jacket cell** and the **primary** ...

the antheridium and **primary cover cell** and the **central cell** in the archegonium.

Antheridia

The antheridia in *Lycopodium* dev- [illegible] gon [illegible] the marginal meristem. In *L. lucidulum* there is intermingling of the two kinds of sex organs. The antheridia are mostly embedded (Fig. 4·18, 4·20) in the tissue of the prothallus.

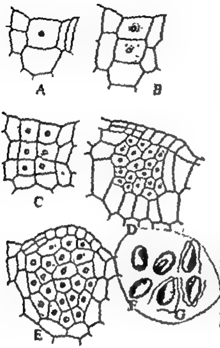


Fig. 4·20 (A—G).
Lycopodium clavatum.
A—E. Various stages in the development of antheridium.
F. Spermatocytes. G. [illegible] matozoids.
(After Bruchman)

Development (Fig. 4·18 & 4·20)

The antheridium arises from a single superficial cell which [illegible] into a [illegible] primary wall cell and an inner primary spermatogenous cell. The **primary wall cell** divides by anticlinal wall to form a one layered wall or the jacket of the antheridium. A triangular **opercular cell** is ulti- [illegible] primary spermatogenous cell divides repeatedly to give rise to a mass of [illegible] cells. The an- [illegible] gonial cells [illegible] spermato- cytes [illegible] androcytes [illegible] sperm mother cells (Fig. 4 [illegible]. In *L. phlegmaria* a single section of the antheridium contains up to two hundred **spermatocytes**. The development of spermatozoid within the spermatocyte has not been studied in detail.

Bruchman has studied the structure of the spermatozoids in *L. clavatum*. It is oval in shape (Fig. 4·20, G) and about twice as long as broad. It is pointed at the anterior end which bears two flagella. The cytoplasm forms the major portion of the spermatozoid and the nucleus lies on one side. It is interesting that unlike all other pteridophytes the nucleus in the spermatozoids of *Lycopodium* does not form a major part of its body. In this respect it resembles the male gametes of some algae. Spessard (1922) studied the spermatozoids of *L. lucidulum* and described the nucleus as elongated and curved. Treub described the spermatozoids of *L. phlegmaria* as elongated and twisted. They resemble the spermatozoids of the bryophytes.

Structure of Mature Antheridium (Fig. 4·18 and 4·20, E)

A mature antheridium is either completey embedded in the tissue of the prothallus (*L. selago*) or slightly projecting. It has a single-layered antheridial wall with a distinct triangular **opercular cell**. The wall encloses a large number of spermatocytes whose protoplasts metamorphose into biflagellate spermatozoids.

It dehisces by the mucilaginisation of the single opercular cell or a group of jacket cells. The spermatocytes containing spermatozoids absorb water, swell up and cause the rupture of the antheridial wall.

Archegonia (Fig. 4·19)

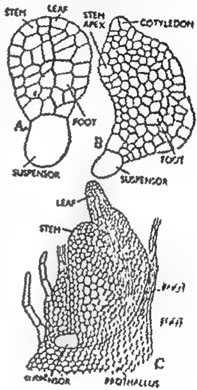
Development. The archegonium arises from a single, superficial archegonial initial. It divides by a periclinal wall into an outer or upper **primary cover cell** (Fig. 4·19, *b*) and a lower or inner **central cell.** The primary **cover cell** divides by two intersecting walls into a quadrant of equal cells (Fig. 4·19, *c*) These four cells are the **neck initials** and divide further by transverse walls to give rise to the neck that varies from three to many cells in height Since the neck is derived from 4 initial neck cells, it has four longitudinal rows. The **central cell** divides by a transverse wall into an upper **primary canal cell** and a lower **primary ventral cell** (Fig. 4·19, *c*). The former may function directly as a single **neck canal cell** in the archegonia of aerial prothalli or it may divide repeatedly by transverse divisions to form a variable number of neck canal cells. In *L. selago* there may be up to seven neck canal cells (Fig. 4·19, *f*). In *L. complanatum* there are 14 to 16 neck canal cells. Freeburg and Wetmore (1957) cultured the prothalli of these two species and reported that the archegonia under cultural conditions have very short necks and only one **neck canal cell.** The primary **ventral cell** undergoes a transverse division to form a lower egg cell and an upper **ventral canal cell** (Fig. 4·19, *g*). In some cases the **primary ventral cell** does not divide and becomes slightly broader and functions directly as the egg cell. Its cytoplasm and nucleus form the female gamete or the **egg** or the **oosphere.**

Structure (Figs. 4·19 *f*; 4·17, F) :—A mature archegonium is distinguishable into a slightly broader and embedded lower portion called the **venter** and a projecting part called the **neck.** The length of the neck varies considerably in the genus The longest neck is found in *L. complanatum* (Fig. 4) and *L. selago* (Fig. 4·19, *f*). Spessard (1922) reported that species with subterranean prothalli bear long necked archegonia with 6—16 neck canal cells. The neck is usually made up of 4 rows of cells each row 3-several cells high ; five longitudinal rows of neck cells have also been reported and such archegonia have very long necks *cf.* bryophyte archegonia). Treub (1884) found that green and surface living prothalli have archegonia with short neck (3—4 cells high) and one neck canal cell. The neck encloses a neck canal which contains one to 16 neck canal cells. The venter has a ventral canal cell and an egg cell. The venter has no

of different species are variable. In some the **foot** becomes massive, in others a specialised structure called the **protocorm** (Fig. 4·17, D, E) develops and in some no such prominent structures become evident. We shall now consider the embryology in different species.

LYCOPODIUM SELAGO AND L. PHLEGMARIA

In these species the foot is quite prominent and develop from the hypobasal quadrants of the octant stage. The epibasal quadrants form an apical meristem by repeated longitudinal and transverse divisions. In *L. phlegmaria* (Fig. 4·22, A—C) the foot is massive as compared to *L. selago*. The foot and the apical meristem divide in different planes, but the divisions are quite regular. The embryo is deeply embedded in the prothallus tissue (Figs. 4·22 and 4·23) and has large cells in foot region. Later divisions result in a curved embryo that bursts through the prothallus tissue in an upward direction. Its apex is the shoot apex made up of a row of meristematic cells. Root differentiates laterally above the foot. Leaf primordia and stem primordia differentiate from the shoot meristem. The leaf primordia arise in a spiral sequence. The shoot and the root regions are transversed by a distinct procambial strand that later mat- into th[illegible] vasculat[illegible] of the root the [illegible] The [illegible] stages are ta[illegible]



wall of its own but is protected and surrounded by the tissue of the prothallus.

Dehiscence. The archegonium when mature dehisces by the disorganisation of the **neck canal cells** and the **ventral canal cell** and opening of the uppermost tier of the neck cells. This creates an open passage for the spermatozoids to enter the neck and reach the **oosphere.**

Fertilisation. It is effected in the presence of water through which the biflagellate spermatozoids swim and reach the open archegonial necks. Bruchmann (1909) reported that the spermatozoids are attracted by a chemical stimulus. He stated that the archegonial necks secrete free citric acid or its salts whose smell attracts the spermatozoids. Only one spermatozoid is able to reach the egg and effect fertilisation. The male and female nuclei fuse together (syngamy) and form a diploid fusion nucleus. So the act of fertilisation switches on the diploid generation. The diploid nucleus with its surrounding cytoplasm and a wall is called **the oospore.**

THE EMBRYO

Treub (1814, 1816, 1890), 1015) and Wigglesworth (1907) hc towards the embryology of the ger in all the species whose embryolog The venter of the archegonium in nuity with the prothallial tissue and the embryology in all of them is **endoscopic** (*i e.*, the shoot apex is directed away from the archegonial neck). The nucleus of the oospore divides by mitosis into two daughter nuclei that are separated from each other by a transverse wall (F 4·21, A). This first division of th eternines the polarity of the results in the formation of an **hypobasal** cell. The cell onial neck is **epibasal** an the **hypobasal cell.** Tl dergoes no further division nction as the suspensor. ivide on or twice. The or t **embryonal** ce emb and divides by tudi walls to form ·21, The **hypobasal** ex the suspensor rise to the foot (**quadrant** forms root (Fig. 4·22, *embryo pushes it deep into the tissue of tl* and away from the archegoni

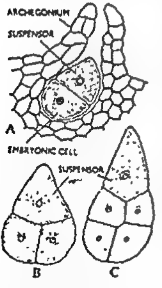


Fig. 4·21. *Lycopodium clavatum.* Early stages of embryo development.

of different species are variable. In some the **foot** becomes massive, in others a specialised structure called the **protocorm** (*Fig.* 4·17, D, E) develops and in some no such prominent structures become evident. We shall now consider the *embryology* in different species.

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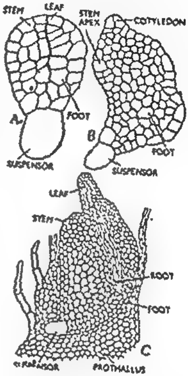

Fig. 4·22. Lycopodium phlegmaria. (A—C) Later stages of embryo development. (After Treub)

In *L. phlegmaria* the epibasal quadrants give rise to the first leaf and the apical meristem. The root initial arises in the leaf quadrant. Further development leads to the emergence of first stem that grows erect and carries the cotyledons above. Later other leaves appear. The root grows down but is short-lived and is soon replaced by adventitious roots.

L. CLAVATUM AND L. ANNOTINUM

In these species the growth of the apical region of the embryo is comparatively very slow and the first two leaves are opposite and not spiral as in *L. selago.* They develop late and are scale-like. The procambial strands also develop late. The massive and haustorial foot, the slow development of the epical region and the procambial strands, and the opposite arrangment of the first two leaves are the main differences between these two species and *L. selago.* In these creeping species first stem is soon replaced by the horizontal stem

wall of its own but is protected and surrounded by the tissue of the prothallus.

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THE EMBRYO

Treub (1814, 1816, 1890), Bruchmann (1910), Holloway (1909, 1915) and Wigglesworth (1907) have made significant contributions towards the embryology of the genus *Lycopodium*. The initial stages in all the species whose embryology has been worked out are similar. The venter of the archegonium in all the species is in cellular continuity with the prothallial tissue and the embryology in all of them is **endoscopic** (*i.e.*, the shoot apex is directed away from the archegonial neck). The nucleus of the oospore divides by mitosis into two daughter nuclei that are separated from each other by a transverse wall (Fig. 4·21, A). This first division of the oospore determines the polarity of the embryo. Its results in the formation of an **epibasal** and a **hypobasal** cell. The cell next to the archegonial neck is **epibasal** and away from it is the **hypobasal cell.** The epibasal cell undergoes no further division and enlarges to function as the suspensor. Rarely it may divide once or twice. The **hypobasal cell** or the **embryonal cell** gives rise to the embryo and divides by transverse and longitudinal walls to form two quadrants (Fig. 4·21, C). The **hypobasal quadrant** which is next to the suspensor cell divides further and gives rise to the foot (Fig. 4·22, A). The **epibasal quadrant** forms the shoot and the primary root (Fig. 4 22, A). Further growth of the embryo pushes it deep into the tissue of the prothallus (Fig. 4·22, C) and away from the archegonial neck. Later stages in embryology

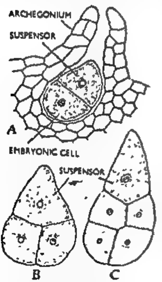

Fig. 4·21. **Lycopodium clavatum.** Early stages of embryo development.

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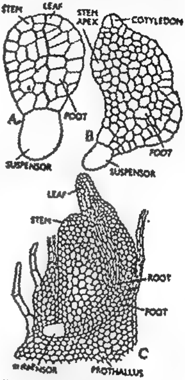

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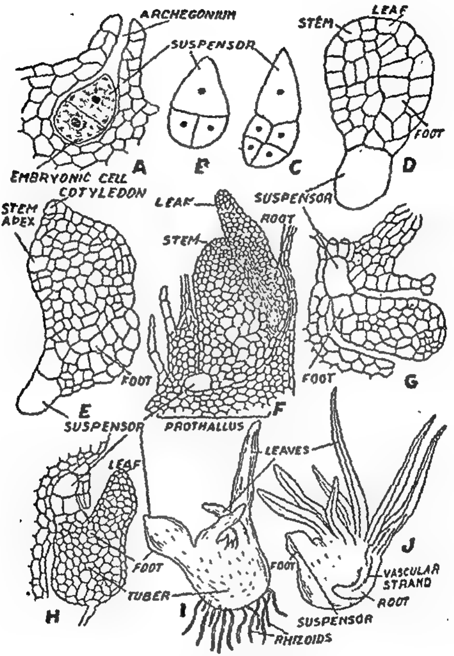

Fig 4·23 (A—J) Embryogeny in *Lycopodium*.

A—C. Three early stages of development of embryo in *L. clavatum*. (After Bruchmann).
D—F. Embryos of *L. phlegmaria* (After Treub).
G—J. Embryos of *L. cernuum*.
G. Young embryo has grown through the prothallus.
H. Embryo with differentiation into *leaf*, *foot*, and tuber.
I. An older embryo with three leaves. Rhizoids have developed from tuber or protocorm.
J. L.S. Older embryo. Vascular strand has started developing. (After Treub).

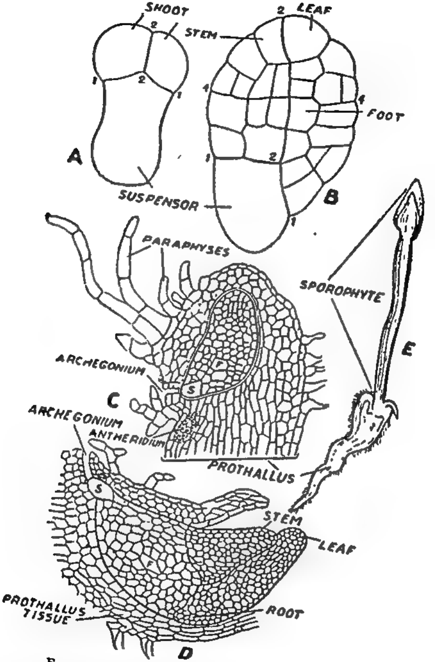

Fig. 4·24 (A—E). Lycopodium selago.

A. Young embryo as seen in L. S. The wall 1—1 has divided it into suspensor segment and shoot segment.
B. L. S. through older embryo showing suspensor, foot, stem and leaf segments. Positions of walls 1—1, 2—2 and 4—4 are clear.
C. Later stage of embryo still enclosed in the prothallus tissue.
D. Mature embryo breaking through the prothallus tissue, S=suspensor; F=foot.
E. A young sporophyte attached to prothallus. (After Bruchmann)

which arises from the base of the former and bears colourless scale leaves that are devoid of midrib and vascular supply. The development is very slow and this young sporophyte depends for years together on the subterranean, gametophyte for nutrition. It takes many years for it to come above ground and become independent.

L. CERNUUM AND L. INUNDATUM

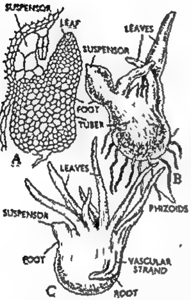

Fig. 4·25. **Lycopodium cernuum.**
(A—C). A. Young embryo has grown through the prothallus.
B. Embryo showing differentiation into leaf, foot and tuber.
C. An embryo with three leaves Rhizoids have developed from the tuber a protocorm.

These species are characterised by the development of a tuberous mass of cells called the **protocorm** from the epibasal quadrant (Fig. 4·25). It is made up of undifferentiated mass of parenchymatous cells It bears numerous rhizoidal hair that attach it to the soil. The cells at the base contain a symbiotic fungus. A conical outgrowth develops on the upper surface of the protocorm. It soon grows into a cylindrical green leaf or **protophyll.** This is followed by the formation of an indefinite number of **protophylls,** without any regular arrangement (Fig. 4·25, B, C). Both the protocorm and the protophylls lack a vascular strand. They are green and the protophylls possess stomata. The protocorm with its protophylls soon loses contact with the prothallus. It is at a later stage that the **shoot apex** can be recognised at the distal end of the protocorm. The shoot apex develops close to the last formed protophylls. It soon becomes prominent and bears young leaves in a normal phyllotactic sequence. At a later stage a primary root also arises and penetrates the soil. It is exogenous in origin. Procambial strands also develop in the young sporophyte and later mature into vascular tissue.

Morphology of the Protocorm

Treub regarded protocorm as a primitive structure that has been retained as an ancestral feature by some contemporary species. He visualised that it must have been present in the ancestral vascular plants. Treub's view has not received popularity and is now regarded as of historical importance only.

[illegible] growth' that deve- [illegible] the prevailing envi- [illegible] ortance to this stru- [illegible] to soil and has no phylogenetic importance.

Browne (1913) regarded the protocorm as a modified and a reduce[d] stem.

Holloway regarded the protocorm as a specialised structure that helps the young sporophyte to perennate over dry season and that it has no phylogenetic significance.

Wardlaw (1935) regarded the protocorm as a modified shoot. He is of the opinion that its regular appearance in certain species of *Lycopodium* is not due to any environmental effect but to certain genetic factors that must be involved in its persistence in these species. He attributed the development of protocorm to certain metabolic conditions of the prothallus and young sporophyte. According to him carbohydrate and nitrogen ratio (C/N) is responsible for the development of localised swellings in the embryo. In case the embryo received a balanced nutrition and C/N ratio is normal the embryo produces no swellings and produces normal elongating leafy shoot. In case the embryo receives unbalanced nutrition and C/N ratio is high the organisation of the young shoot apex is delayed and protocormous outgrowths develop. Wardlaw states that in *L cernuum* and *L laterale* (protocormous species) the genes which determine protein synthesis at the shoot apex are ineffective in the beginning. This leads to the delay inthe development of shoot apex and aids in the formation of a new structure called the **protocorm.** Later the green **protophylls** and **protocorm** as a result of their photosynthetic activity produce certain essential metabolic products that lead to the growth of the shoot. The ineffective gene is thus switched on to activity.

Deviations from Normal Life Cycle

Occurrence of the phenomenon of apospory and apogamy in *Lycopodium* have not so far been reported in nature. Recently Freeberg (1957) was able to induce apogamy in *L. complanatum*, *L. cernuum* and *L selago*. He was able to grow these species under cultural conditions by germinating their spore on culture media. He got full-fledged gametophytes that bore sex organs and produced after normal fertilisation, embryo and young sporophytes. During his experiments he found that under conditions unfavourable for fertilization (absence of water) the gametophytic tissue produces complete sporophytic plants apogamously. The young sporophytes arise apogamously from the tips of the branches of porthalli. Gametophytic tissue was also induced to produce a single leaf. Such apogamously produced sporophytes were also observed, in rare cases, to produce from the stem a gametophyte like outgrowth. Only one such case of formation of aposporous gametophyte was observed by Freeberg (1954). De Moggio (1964) induced apogamy in the gametophytes of *L. obscurum* by supplying coconut milk or sucrose or both to the nutrient medium. He was able to induce the formation of roots of buds in the gametophytic callus of this species.

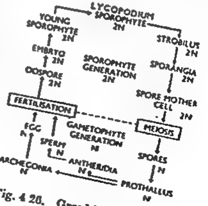

Fig. 4 26. Graphic representation of life cycle of **Lycopodium.**

Economic Importance

The spores of *Lycopodium inundatum* and some other species yield 50% fixed oils. They are much used as cover for pills, as a diluent for insufflations, and as a dusting powder for abraded surfaces. In industry they are used for making pattern molds; because of their inflammability they are used in flares, fireworks and tracer bullets.

CHAPTER V

LYCOPHYTA (contd.)

LIGULOPSIDA

The class includes all heterosporous forms with ligulate and microphyllous leaves. It includes four orders. These are: the **Isoetales**, the **Selaginellales**, the **Pleuromeiales** and the **Lepidodendrales**. The last two are extinct orders. The first two include living as well as extinct members.

ISOETALES

It includes a single family **Isoetaceae**, that is characterised by (*i*) a corm-like axis that bears numerous leaves, (*ii*) apical growth by a group of meristematic cells, (*iii*) perennial root producing meristem, (*iv*) secondary growth, (*v*) small and ligulate leaves, (*vi*) two types of spores, (*vii*) endosporic gametophytes and (*viii*) multiflagellate spermatozoids. *Isoetes* and *stylites* are the living, and *Isoetites* is the extinct members of the family. *Stylites* has two species found in Peruvian Andes. It differs from *Isoetes* in having elongated stem and unbranched roots. Rauh and Falk reported in 1959.

ISOETES

It includes about 75 species (Airy Shaw in Willis 1966) that are familiarly known as **'quillworts'** due to their narrow and elongated grass-like leaves with broad and spathulate bases. Majority of the species are found in Europe and North America. In India four species have been recorded. The most common out of them is *Isoetes coromandelina* (Fig. 5·1). The other three are *I. sampathkumarani*, *I. indica*, and *I. mirzapurense*. Recently *I. panchananii* has been recorded from Pachmahri hills (Bir, 1973).

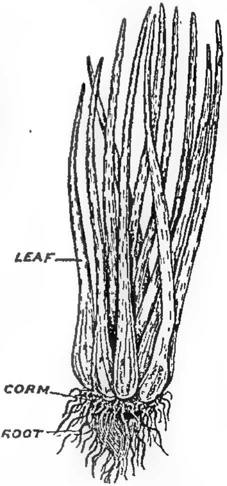

Fig. 5·1. Isoetes corommandelina. A complete plant showing habit.

The sporophyte

Habit and Habitat. The common Indian species *I. corommand-*

taxis. The lobes grow more in breadth by the dilatation of the tissue and vary from 0 5—4 centimetres in width. Grooves develop by the appearance of longitudinal slits between the lobes. The tissues are sloughed off in the form of characteristic 'caps' or 'shoulders' (Eames, 1936) that appear on the upper margins of the axis (Fig. 5·2). This

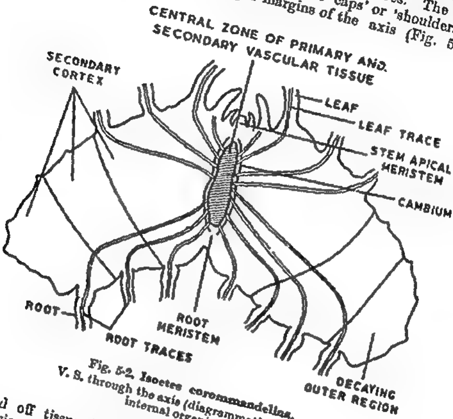

Fig. 5·2. Isoetes coromandelina. V. S. through the axis (diagrammatic) showing internal organisation.

sloughed off tissue includes the bases of the leaves and the roots of the previous year and undergo decay at the end of the growing season. The growth in length of the axis is very slow and it effected by a group of meristematic cells that lie sunken in a groove formed by the greater growth of the surrounding tissue.

Karrfalt and Eggert (1972) studied the development roots and lobes in some species of *Isoetes* (*I. saccharata* and *I. tickermanii*). They ascribe their formation to two developmental processes. They found that there is a row of tangentially elongated cells at the base of the furrows. They perform the mechanical function of separating the lobes. "Progressive rupture of these cells from surface to deeper layers maintains the depth of the furrow. This layer of elongated cells becomes double and by meristematic activity produce a new lobe in the region between the two layers. New lobes also appear by the development of a furrow between the two bands.

Dichotomous branching has also been observed in some plants, but the dichotomy never becomes prominent due to the the very

elina grows wild along the Coromandel Coast, Madras, Bombay, Banaras, Baroda, Serampur in Bengal, along the banks of river Jamuna at D[illegible] [illegible] land at Meerut. The Indian species are [illegible] *Isoetes coromandelina* is perennial [illegible] that starts about mid-October after the monsoon and continues till March. It is mostly amphibious in existence and is common along the edges of ponds, pools and rivers. It also grows in shallow water with portion of leaves projecting above water. *I. panchananii* is also amphibious.

The American species *I. engelmanni* is a partially submerged aquatic *Isoetes japonica* grows submerged in water. *I. butleri* is terrestrial.

The sporophyte of *Isoetes*, when growing under natural conditions, gives the appearance of a liliaceous or a graminaceous monocotyledon. Its characteristic leaves that arise from a subterranean and bulbous axis (Fig. 5 1) simulate in appearance with those of the sterile lilies or sterile and tufted grasses. The underground portion of sporophyte has been given the names of "Corm" and 'rhizome, because it is thick, reduced and looks like a condensed rhizome. These terms have been considered to be inappropriate by Eames (1936). He uses the term **axis** for this underground stem like part. The axis is clearly distinguishable into an upper leaf bearing part [illegible] roots. The former is [illegible] is greatly [illegible] each other [illegible] **zomorph** and the line of demarcation between the [illegible] is obscure.

Axis

In young [illegible] and is covered with the leave[illegible] (Figs. [illegible] 1 and 5·2). In older [illegible] of lobes vary from two to three and even four or five in [illegible] (*I. saccharata*). The grooves between the lobes deepen as the axis increases in age and make them (lobes) prominent (Fig. 5 2) Brongniart (1828, p. 28) related the lobed axis of *Isoetes* to the **Stigmarian** axis. Magdefrau (1932) regarded *Isoetes* as [illegible] remnant of Lepidophytes, the Mesozoic forms *Pleuromeia* a[illegible] inter-mediate links This view is [illegible] develop due to the action [illegible] basal side, but only due to the local formation of [illegible] tissues by the cambium. In *Stigmaria* the lobes of the axis grow by the activity of a vegetative cone ,so they cannot be related to the lobed *Isoetes* axis.

The place where the lobes arise is determined by the phyllotaxis of the young plants. In distichous plants the grooves alternate with the leaf orthostichies under which the lobes are formed Such a position was first observed by Al Braun in 1847. Once the lobes are formed they maintain their position even on change of phyllo-

taxis. The lobes grow more in breadth by the dilatation of the tissue and vary from 0·5—4 centimetres in width. Grooves develop by the appearance of longitudinal slits between the lobes. The tissues are sloughed off in the form of characteristic 'caps' or 'shoulders' (Eames, 1936) that appear on the upper margins of the axis (Fig. 5·2). This

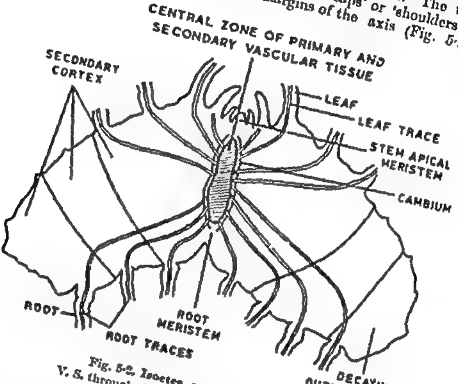

Fig. 5·2. Isoetes coromandelina. V. S. through the axis (diagrammatic) showing internal organisation.

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Dichotomous branching has also been observed in some plants, but the dichotomy never becomes prominent due to the the very

slow growth of the axis. It is evident only by the presence of two crowns of leaves.

Morphological Nature of the Axis

Regarding the morophological nature of the axis, several views have been advanced. Braun (1847) believed that the lower part of the *Isoetes* stock base was nothing but a telescoped main root. He based his view on the basipetalous development of the new roots. Scott and Hill (1900) studied the development of roots in *I. hystrix* and disagreed with Braun. Lang (1915) after intensive anatomical studies concluded "that the recognition of the lower region of the stock of *Isoetes* as a rhizomorph in some way correlated with the upwardly growing shoot appears to be justified". Liebig (1931) declared that all her median longitudinal sections of the stock are proofs of Braun's thesis. West and Takeda (1915) hold another

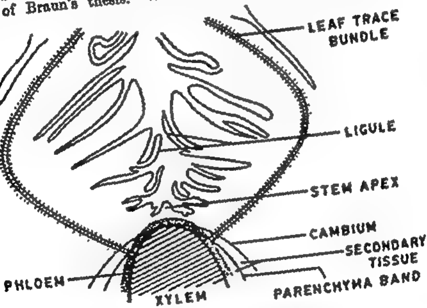


Fig. 5·3. **Isoetes coromandelina.** L.S. through the axis (upper part) showing the stem apex, vascular region and arrangement of young leaves. Also note the ligules. (After Bhambie)

view. They regard the downward growing rhizomorph as an organ *suigeneris*. Eames (1936) regards the axis as differentiated into an upper leaf bearing portion called the *stem* and a lower root bearing portion called the **rhizomorph**. Schouto (1938) regards the *Isoetes* axis as a stem and states "...that the stock base of *Isoetes* is peculiar in its constantly tearing furrows, a feature connected with the formation of local humps of secondary tissue, the lobes. Roots are formed, as always in all plants, in any suitable place; the presence of the furrows and the lack of new higher stem parts cause these suitable places to be found in an unusual arrangement." He used the term **stock base** for the axis.

Barclay (1931) stated that there is an intergradation from a single apical cell to a general meristematic group. Bruchmann (1897) reported apical growth in *Selaginella spinulosa* by a general meristem. Strassburger (1891) reported the presence of two initial apical cells in *S. wallichii*. Williams (1931) also reported two apical initials in *S. grandis*. A single apical cell has been reported in some species of *Selaginella* by Barclay (1931), Pfeffier, Treub and Hofemeister.

Root

In the embryo the first root arises laterally and exogenously (Farmer, 1890). It is provided with root hair and with a root cap. The position of the later roots that arise endogenously is always related to the place of the grooves. These roots, according to most of the authors, are formed in series along the sides of the grooves and are, therefore, in the same position as the orthostichies. This is because the grooves appear in the same position as the orthostichies. *In each groove or a furrow the roots arise in an acropetalous* succession, *i.e.*, the youngest is near the stem apex or the end of the groove. West and Takeda (1915) reported that all the roots in the furrow are of the same age—a statement that is very difficult to believe. They have not given any observations in support of their statement. Scott and Hill (1900) have clearly shown the acropetalous development of the roots in *I. hystrix*. West and Takeda state that in *I. japonica* new roots develop on the sides of the grooves near the base. When new roots develop in the next season the older ones are pushed outwards towards the ends of the groove (stem apex). Accordingly the younger roots are near the centre of the groove and older ones at the ends of the grooves. *These observations* are quite contrary to those of Scott and Hill.

The roots branch dichotomously after emerging from the **rhizomorph** (lower part of the axis) ground tissue. The root apex *has been reported to consist of a group of initials (Farmer, 1890,* Campbell, 1891) that give rise to the root cap, epidermis and cortex. According to these authors the vascular tissues arise from a single initial.

Leaf

The leaves are microphyllous as they are traversed by a single median and unbranched vein. The leaf traces leave no gap in the vascular cylinder of the stem. They vary in length from two centimetres to two feet (*I. engelmanni*). They are arranged in close spirals near the upper end of the axis, *and range in number* from a few to 20. Each leaf has a broad spoon like base and a narrow and linear upper part. The leaf tips are pointed and straight or recurved and sometimes four-angled. The basal, broad portions of the leaves are underground and colourless, whereas the aerial and linear parts are green and photosynthetic. The leaf bases of outer leaves overlap those of the inner leaves and thus give a bulbous appearance (Fig. 5·1). Usually the first formed or the older leaves and those produced at the end of the growing

season are sterile and the rest are fertile, *i.e.*, they bear sporangia and are called **sporophylls.** In some species abortive sporongia have also been noted at the bases of the sterile leaves. So every

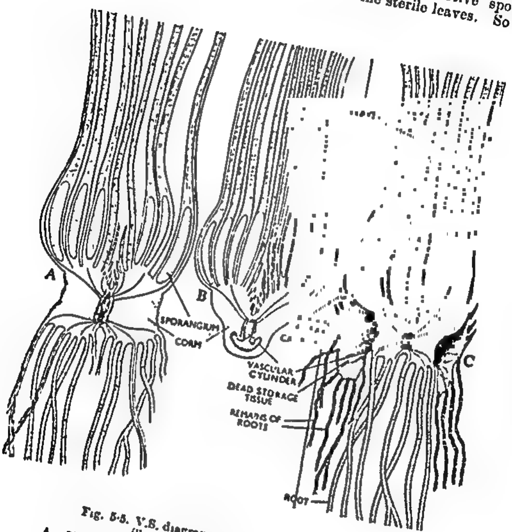


Fig. 5·5. V.S. diagrams through the entire plant illustrating form and structure.

A. V.S. cut at right angles to the basal groove of the "corm" of a young plant, showing sporangia, the apex and the stele of the corm.

B. V.S. in the plant of the groove, the stele appears like an inverted 'T'.

C. Same as A but the plant is older and shows storage region of the corm and dead remains of older tissue (After Eames).

leaf is a potential sporophyll and the entire plant can be regarded as a **strobilus.** Each leaf has, therefore, a lower colourless sporan-

gium bearing (Fig. 5 5) or fertile region and an upper sterile or photosynthetic region. At the junction of the basal, spoon shaped part of the leaf and the upper green part or the blade there is a small depression on the adaxial side. From this pit or depression arises a small ligule (Fig. 5 6).

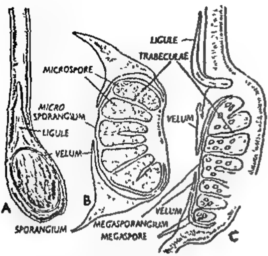


Fig. 5.6. **Isoetes.**

A. Lower portion of the leaf showing ligule and the velum covering the sporangium.

B. T.S. through the sporangial region of the microsporophyll showing a microsporangium with trabeculae.

C. L S. through the megasporangial part of a megasporophyll.

Note the ligule and the velum.

Development of Leaf and Ligule

Leaves originate as small outgrowths that arise by the periclinal divisions of the surface cells of the apical meristem. The outgrowth assumes a crescentic outline in the beginning and soon a group of apical initials appear and initiate growth in length. During earlier stages of growth when the leaf mound is only few cells high, a prominent cell distinguishes itself on the adaxial side near the base of the leaf mound. This cell is the initial of the **ligule** (Smith, 1900) This cell divides periclinally and by repeated divisions gives rise to a filamentous structure that soon grows longer than the leaf primordium (Fig. 5 7, A). Later this filamentous structure, by divisions in various planes and by cell differentiation, ... specialised internal ... the foot of the ligule ... e leaf. This socketed part is covered by a sheath that consists of a single layer of cells continuous externally with the leaf epidermis and internally with the epidermis of the ligule. Dunlop (1949) reported the presence of **casparian strips** in the cells of the sheath in *I. macrospora*. In *I. engelmanni* Smith (1900) described the foot region of the ligule to be a massive structure with its sides growing upwards and downwards forming pairs of horn-like structures.

The ligules are regarded as secretory structures that secrete water or mucilage and keeps the leaves and the sporangia moist.

ANATOMY

Axis

As stated before, the leaf bearing region of the axis is called **stem.** It has its own growing point The lower root bearing part

which is called the **rhizomorph** also has its own growing point. Growth in length of the axis is very slow, but increase in diameter is considerable. This circumferential increase is due to the activity of cambium, *i.e.*, the axis exhibits secondary growth. The anatomy of

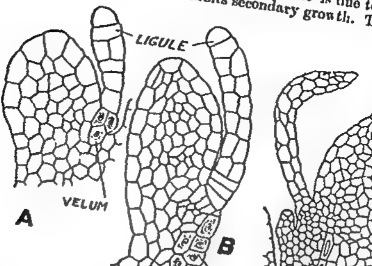


Fig. 5·7 (A—E). **Isoetes coromandelina.** Various stages in the development of the ligule and the velum. A young sporangium also seen developing below the velum in E. (After Ekambaram and Venkatanathan).

the axis is complicated and is variously interpreted. The stelar arrangement in the axis is typically protostelic with a central core made up of xylem (tracheids and parenchyma) surrounded by phloem, which in turn is surrounded by an extra stelar layer of cambium. External to the cambium are the cortex and epidermis. The stele of the axis

in a longitudinal section appears like an inverted 'T'. The vertical arm of the 'T' represents the stele of the upper region of the axis (stem) and the horizontal arm represents the stele of the rhizomorph. There is a prominent constriction between the two steles (Fig. 5·2). The xylem is composed of tracheids and xylem parenchyma. The phloem is made up of a few layers of prismatic cells. The cambium is absent opposite the apical meristems of stem and the rhizomorph and is, therefore, not a complete cylinder (Fig. 5·2).

The extra-stelar cambium cuts off cells both towards its inner side and outer side (Fig. 5·2). Those cut off towards the inner side

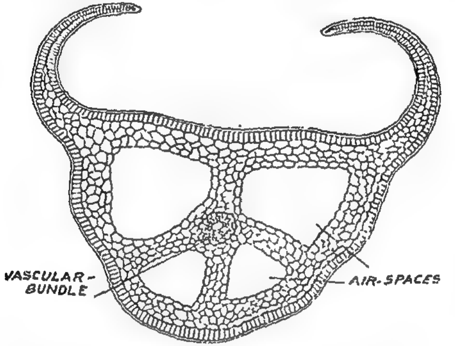


Fig. 5 3. Isoetes coromandelina, T.S. through leaf.

become changed into phloem (West & Takeda, 1915) or sometimes into phloem and xylem elements both (Scott and Hill, 1900). In some species the inner cells cut off by the cambium develop into tracheids and parenchyma (Stokey, 1909). Esau (1953) examined the cell cut off towards the inner side in I. *howellii* and found them to be secondary phloem. The **sieve cells** have **sieve areas** on their lateral and end walls. The cells cut off towards the outer side develop into secondary cortex. The cells of the secondary cortex store food material and for [illegible] parenchyma. Every year new storage parenchyma is f[illegible] one is pushed outward and is [illegible] 'caps' or 'shoulders'. The sloughed off tissue also [illegible] p[illegible]ons of secondary vascular tissue. The surface layers that persist become suberised. Numerous leaf traces arise from the stele of the *stem*, one going to each leaf (Fig. 5-2). In the rhizomorph root traces pass from the stele to the roots (Fig. 5-2).

Leaf

A transverse section of the leaf (Fig. 5-8) shows an outer layer of compactly arranged cells called the **epidermis**. It is covered by

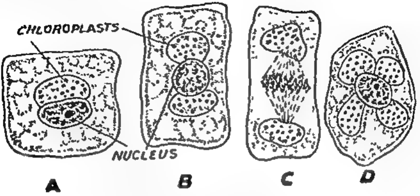


Fig. 5·9. Isoetes melanopoda.
A. A cell from leaf with one chloroplast. B. Cell with two chloroplasts, one on either side of the nucleus. C. Same as B. D. Cell with 4 chloroplasts arranged around the nucleus. (After Ma)

a thin cuticle. Next to it is the mesophyll that is not differentiated into palisade and spongy parenchyma. The cells contain chloroplasts (Fig. 5·9) which range in number from one to four per cell. The chloroplasts are very close to the nucleus. In *I. melanopoda* there may be one to four plastids in each cell (Fig. 5·9). The mesophyll is traversed by four longitudinal air spaces that are separated from each other by several layered thick partitions. The air spaces or the lacunae are divided by a series of partitions or diaphragms (Fig. 5·8). There is a single central collateral vascular bundle.

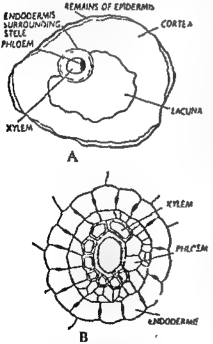


Fig. 5·10. Root of Isoetes sp.
A. A diagrammatic coss-section showing internal structure.
B. Stele shown in details.

In the young sporophytes the leaf has only two lacunae. In the submerged species the epidermis lacks stomata whereas in the amphibious and terrestrial species stomata are present.

Root

A transvere section of a root (Fig. 5·10) reveals the usual tissue systems, *viz.*, the epidermis, the cortex, the endodermis and the stele. **epidermis** is single layered

temporary. The **cortex** is made up of many layers of thin-walled cells and its innermost layer is called the **endodermis.** The endodermis possesses distinct **casparian strips.** The cortex surrounds a large air cavity (Fig. 5·10).

The vascular cylinder is present on one side of the cavity and is attached to the cortex on that side (Fig. 5·10). The stele consists of primary xylem and phloem that are collateral in arrangement. The phloem is oriented towards the cavity.

Vegetative propagation

Vegetative propagation is rare in *Isoetes.* Formation of adventitious buds has been reported in some species. Solms-Laubach (1902) was able to induce the formation of adventitious buds in *Isoetes laustris* and *I. duriei.*

REPRODUCTION

The sporophyte produces two kinds of spores and is thus **heterosporous.** The microspores are produced in **microsporangia** that arise at the bases of **microsporophylls** (Fig. 5·5). The **megaspores** are formed in megasporangia that are borne at the bases of **megasporophylls** (Fig. 5·5). The megasporophylls form the outermost whorl (Fig. 5·5) and are followed by an inner whorl of microsporophylls which in turn surround the innermost sterile leaves that may in some species bear abortive sporangia. At the end of the growing season and during the resting period the megasporophylls and the microsporophylls degenerate or die whereas the innermost sterile leaves may continue to live. They act as outermost whorl during the next season and generally disappear before the new leaves appear. In *Isoetes coromandelina* purely megasporophyllous plants are found in abundance (Ekambaram and Venkatanathan, 1933; Bhambie, 1957).

Arrangement of Sporophylls

The arrangement of sporophylls has been studied in detail in some species by various authors. A brief resume is given here The Indian species *Isoetes coromandelina* is very interesting. The first account of the arrangement of sporophylls in the species was given by Pfeiffer (1922). She found that majority of the plants bore only megasporophylls. In some specimens she found groups of microspores sticking to the bases of sporophylls. She was unable to observe the complete and intact microsporangia. Ekambaram and Venkatanathan [illegible] found that the first two [illegible] nption of' growth by the [illegible] rangia. The leaves that arise later are all fertile. They observed two kinds of plants: (*i*) bisporangiate plants and (*ii*) megasporangiate plants. The megasporangiate plants are found in abundance and bear *only* megasporophylls with megasporangia at their bases. The megasporophylls are arranged in close spirals. In the bisporangiate plants there are only one or two microsporophylls and the rest are all megasporophylls.

These plants are less common and were encountered during early rainy season. The ratio of bisporangiate plants to megasporangiate plants is 2 or [illegible] to 50. There is no external difference between the two kinds of plants. The first microsporophyll develops after the formation of two or three megasporophylls. In case there are two microsporophylls, the second one does not develop immediately after the first but it comes up later, *i.e.*, after the formation of a few megasporophylls. The megasporophylls that develop late have megasporangia with immature megaspores or do not form megaspores at all. This is probably due to onset of unfavourable conditions (Ekambaram and Venkatanathan, 1933).

In *Isoetes lacustris* the innermost leaves are sterile, the middle ones are microsporophylls (*i.e.*, they bear microsporangia) and the outermost are megasporophylls (they bear megasporangia). Gluck (1924) studied various species of *Isoets* and observed a number of variations in the arrangement of the microsporophylls and the megasporophylls. His results reveal that there is no regularity in the arrangement of the sporophylls with respect to each other. Wilson Smith (1900) also observed irregularity in their arrangement. He observed that in *Isoetes engelmanni* "it was not at all unknown to find several megasporophylls among the microsporophylls. Some plants which have been growing in the laboratory for seven or eight months formed only megaspores; some others though producing a few microsporophylls failed to bring any microspores to perfection". West and Takeda (1915) stated that it is erroneous to say that there is any regularity in the arrangement of the sporophylls. They regard the textbook version that inner leaves are sterile and are followed by microsporophylls and megasporophylls, as absolutely wrong. They state, "when the plant is dug up late in the year it often happens that the sterile leaves of the outermost whorl of the rosette have by that time decayed away; under these circumstances sporophylls are found on the margin. But if such a leaf rosette is carefully dissected, young sterile leaves will be found in the centre; these are generally regarded as belonging to the present season's growth but actually represent the outermost circle of next year's growth". They studied in detail the morphology and ontogeny in *Isoetes japonica*, and found no regular sequence in the development of sporophylls. They are irregularly distributed.

The Velum

It is a characteristic structure that arises below the ligule and develops very early in the history of development of the leaf. It originates from the tissue between the ligule and the sporangium (Fig. 5·7, A—E and 5·11, A). The velum is a lobed structure. The upper lobe or the **labium** (Braun, 1863) grows obliquely upwards and remains short whereas the lower lobe grows downwards and is continuous with tissues of the leaves at the sides. In some species the lower lobe covers the entire sporangium, like a pouch, leaving only a small slit-like aperture below. Such a condition is found in the terrestrial species, *e.g.*, *Isoetes hystrix*. In aquatic species the

velum is not so well developed and the lower lobe only partially covers the *sporangium*. In *Isoetes coromandelina* the lower lobe is completely absent. The same is the case in some other species also.

Several conflicting accounts regarding the development of velum have appeared. Majority of them describe that velum originates from the upper tiers of cells resulting from the divisions of the sporangium initials. Hofmeister (1862) describes that velum separates from the sporangium by the earlier divisions of the sporangial initial. Wilson Smith (1900) regards it as the sterilised portion of a sporogenous tissue, or a part of the 'sporangium fundament'. Braun (1863), Scott and Hill (1900) describe that in *I. hystrix* velum has an origin from a tissue quite distinct from that of the sporangium. Ekambaram and Venkatanathan (1933) studied the development of velum in *I. coromandelina* (Figs. 5·7 and 5·11) and observed that it has an independent origin. They point out that velum originates much earlier than the appearance of sporangial initial. Sporangial initial originates later below the velum, when the latter is only 6—8 cells (Fig. 5·7) high. The three initial cells of velum later divide and from a group of 5-6 cells (Fig. 5·7, B) which later grow into a small tongue-like structure (Fig. 5·7, C) that runs obliquely upwards. A group of sporangial initials (Fig. 5·7, E) appears later at the base of the sporophyll below the velum. These cells have larger *nuclei* and

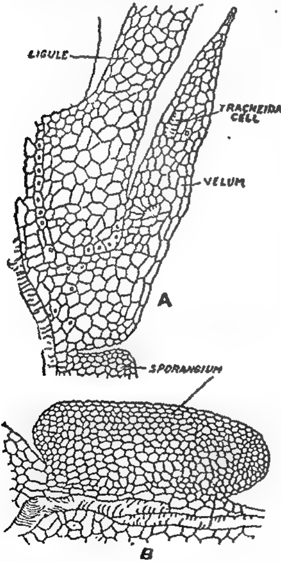


Fig. 5·11 (A—B). **Isoetes Coromandelina.**
A. [illegible]
B. [illegible]

denser cytoplasmic contents. The velum has distinct epidermal layers at its free portion. The tiss
made up of large cells that are colo
contents when mature Some of
cells with spiral or annular thickenings (Fig. 5·11, A). Such cells make their appearance first in the upper free portion of the ligule and later in the lower portion. The tracheidal cells of the velum have a definite connection with the vascular bundle of the leaf by "a narrow strip of tracheidal cells" (Ekambaram and Venkatanathan, 1933). Wilson Smith (1900) denies any such connection in *I. echinospora* and *I. engelmanni*. In *I. coromandelina* velum was also found to develop on the sterile leaves.

Ekambaram and Venkatanathan (1933) regard it as a purely vegetative structure because of the following characteristic features :

1. It originates quite independent of the sporangium.

2. Its formation in sterile leaves.

3. Presence of connections between the vascular tissue of the leaf and the tracheidal cells of the velum.

These authors regard the velum as a vestigial structure. They state, "The exact homologies and functions of this structure remain unknown for want of satisfactory evidence either from the fossil or living allies of the genus. The presence of the tracheidal network as a branch of the leaf trace bundle indicates that the velum, unlike the ligule which presumably is a later interpolated structure, is a more fundamental part of the leaf, which in the course of evolution has degenerated. The velum according to this view will represent a vestigial structure."

Sporangia

(*a*) **Position and Structure** (Figs. 5·7, 5·11, 5·12, 5·13, 5·14). In *Isoetes coromandelina* the sporangia originate from a group of cells below the velum. They have no ontogenetic connection, whatsoever with the velum. Some authors describe the origin of velum from sporangial initial (Hofmeister, Wilson Smith). Others (Ekambaram and Venkatanathan, Braun ; Scott and Hill) deny any developmental connection between the sporangium and the velum. In some species the lower lobe of the velum covers the entire sporangium except near its base. In others the sporangium is only partially covered. In the Indian species, *I. coromandelina* the lower lobe of the velum is absent and the sporangium is therefore naked.

The sporangia are sessile and are largest among the living vascular cryptogams. They are almost oblong-rounded in shape and vary in length from 4 to 10 mm. They arise at the base of the sporophylls and are, therefore, foliar in nature. They occur singly and are adaxial. The mature sporangium is surrounded by a sterile jacket of three or four layers of cells. The innermost layer is made up of large and transparent cells with distinct nuclei. This

called the **tapetum**. In some species (*I. nuttallii*) the tapetum is two-layered. The cavity of the sporangium is incompletely divided by transverse partitions of sterile tissue called the **trabeculae**

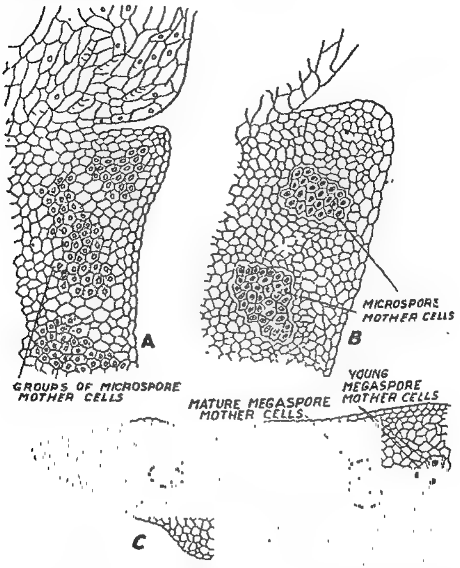


Fig. 5·12 (A—C). Isoetes coromandelina. Stages in the development *of sporangia.*

A, B [illegible] stages in the development of a microsporangium. Groups

C, [illegible] um. The wall [illegible] yet.

(Fig. 5·14). These trabeculae are numerous in megasporangia and comparatively fewer in microsporangia. The incompletely *divided sporangial cavity* is full of sporogenous tissue which later distinguishes into **spore mother cells** or the **sporocytes.** The sporo-

genous cells adjacent to the trabeculae and sides of the sporangium become modified into tapetal cells. The rest of the sporogenous cells function as potential sporocytes. At this stage the micro and megasporangia follow a different course of development.

The microsporangia contain a larger number of microspore mother cells, which undergo meiosis and produce 3000,000 to 1,000,000 microspores. The megasporangia contain a limited number of megaspore mother cells usually 40 to 80. The number of megaspores varies between 160—320 per megasporangium.

(b) **Development** (Figs. 5·7, 5·11—5·14). The development of the two kinds of sporangia follows a similar course of events upto the differentiation of fertile sporogenous tissue. Both the kinds of sporangia originate from the uppermost layer of cells of the sporophyll between the velum and the base of the sporophyll (Fig. 5·7, E). This layer of cells divides in all planes to give rise to a group of sporangial cells. These cells are similar and undifferentiated. No demarcation between the peripheral jacket cells and central sporogenous cells exists during early stages of development. Periclinal divisions have, no doubt, been observed in the outer cells of the undifferentiated mass. These divisions add a large number of cells to the inner mass of cells leading to the formation of a young sporangium composed of a mass of uniform cells (Fig. 5·11, B). In *I. nuttallii* (G.M. Smith, 1955) the young sporangium, at this stage, shows a differentiation into a single outermost layer of cells from a large group of central cells (Fig. 5·13). The latter have distinct nuclei and d... regarded as sporogenous ce... has been observed in *I.* ... nathan, 1933). Goebel (18... an early differentiation between the sterile jacket layers and the central sporogenous tissue in *Isoetes* sporangia. Such an observation has not been confirmed by any of the further studies.

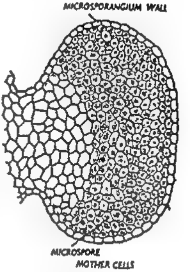


Fig. 5·13. Isoetes nuttallii. A young microsporangium (After Smith)

The uniform ...
a fairl...
and fc...
These ... under two separate headings :

The Megasporangium

In case the sporangial mass is destined to develop into a megasporangium, the following changes take place in it :—

1. Some individual cells or groups of 2 to 3 cells (*I. coromandelina*) enlarge in size. Their nuclei attain larger size and the cytoplasmic contents become denser so that they can be easily distinguished from the surrounding cells (Fig. 5·12, C). These cells are the 'potential megaspore mother cells'.

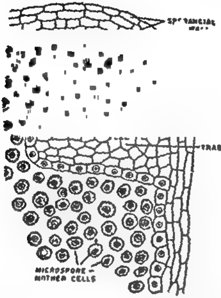


Fig. 5·14. **Isoetes.** A cross-section through older microsporangium with trabeculae, tapetum, wall layers and mother cells.

2. All the potential megaspore mother cells are not capable of reaching maturity. Their differentiation is followed by a considerable enlargement of the sporangium. The megaspore mother cells also enlarge considerably.

3. Some of the megaspore mother cells stop growing. Their contents become less dense and vacuolated. Besides this, a number of mother cells become abortive. These abortive mother cells divide and redivide to form groups of sterile cells. The functional mother cells keep on increasing in size and become rounded or elliptical in shape.

4. *After the functional mother cells have reached maturity* and are ready to divide and produce spores, there is differentiation of the sterile tissue into tapetum, trabeculae and jacket cells. The outermost three or four layers of sterile cells differentiate into the jacket of the sporangium and the tapetum. The abortive mother cells form strands of sterile cells that become differentiated as trabeculae. The sterile cells around the trabeculae also differentiate into one to two or
layers around the
sporangial wall.
anathan, 1933) some sterile cells surrounding the megaspore mother cells degenerate and are completely dissolved to form cavities of the

sporangium. After the formation of these cavities the trabecular cells elongate and form distinct trabecular strands.

5. The megaspore mother cells undergo meiosis and form tetrads of haploid megaspores. Each megaspore mother cell has a distinct *centrosomic plastid*, which later on divides into four such bodies. The four haploid nuclei formed as a result of meiosis separate into haploid cells by cytokinesis. Cytokinesis is accomplished by the [illegible] the nuclei (Fig. 5·15, A). Later [illegible] s separating the four cells still [illegible] cgaspore mother cells (Fig. 5·15, D). *Each of the four daughter cells* secretes a wall around itself and contains a plastid body. These cells *now grow in size* and their cell walls also undergo changes. These cells become thick-walled megaspores. They are arranged in tetrachedral tetra [illegible] the [illegible] pore [illegible] is finally differentiated into three layers. The megaspores are now mature. The wall of the megaspore mother cell surrounding the 4 megaspores disappears so that the megaspores lie free in the cavity of the megasporangium. S.C. Verma (1960) reported an asynaptic triploid individual of *I. coromandelina* from Meerut. This plant produced only megaspores. The second meiotic division is absent but wall formation takes place froming tetrads of two nucleate and two enucleate megaspores. In this case cytokinesis takes place without any regard to the number of nuclei *present in the megaspore mother cell. This curious* feature is suggestive of that cytokinesis and karyokinesis which are normally coordinated with each other, are in this case quite distinct and independent.

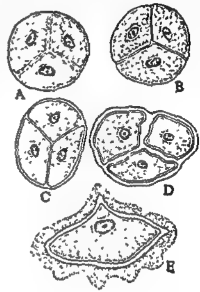


Fig. 5·15 (A—E). **Isoetes coromandelina.** Stages in Megasporogenesis. (After Ekambaram and Venkatanathan)

The Microsporangium

In the microsporangium the sterile sporangial mass differentiates into groups of microspore mother cells and sterile cells (Fig. 5·12, A, B). All the microspore mother cells are functional and undergo reduction division to give rise to an exceedingly large number of microspores (3,00,000—1,000,000 microspores per microsporangium). There is absolutely no degeneration of the microspore mother cells. The sterile *cells around the microspore mother cells* differentiate into trabeculae. Wall layers and tapetum are formed in the same fashion as in the megasporangium. After the formation of micro-

spores the *sterile* cells around them lose their contents and ultimately disintegrate so that the microspores lie free in the cavitities between the trabeculae.

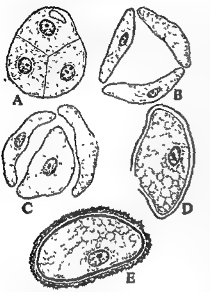


Fig. 5·16 (A—E). Microsporogenesis in **Isoetes coromandelina** (After Ekambaram and Venkatanathan)

The microspore mother cells also contain a polar plastid which divides into 4 similar bodies that are *distributed one each in the resulting* haploid cells. They, no doubt, disappear in the mature microspores. After the completion of meiosis, the haploid daughter protoplasts separate, *by the formation of cell plates* and their resultant splitting (Fig. 5·16). Later they mature into microspores that separate and are set free from the surrounding microspore mother cell wall. At this stage they are more or less semilunar in shape (Fig. 5·16, D, E). Later they become bean-shaped and their cell walls become differentiated into three layers.

Dehiscence of the sporangia

The sporangia in *Isoetes* are indehiscent and the two types of spores (micro- and megaspores) are liberated only when the sporophylls decay after the end of the growing season. Osborn (1922) reported that in *I. drummondii*, that grows in vernal pools, with its axis buried completely in the soil, the spores are exposed or brought [illegible] ...lls of the bases of [illegible]

tissue of the sporangium except the wall and the bases of the sporophylls. They observed that the sporangial walls remain intact and the spores are liberated by the breaking up or by the decay of the portions of the sporangia attached to the sporophyll base.

Spores are mostly wind disseminated. They are also carried by water in aquatic species. Earthworms have also been reported to carry the spores from place to place.

Structure of the Spores

(a) *The megaspores.* The megaspores are usually white, gray or black in colour. They are tetrahedral in shape (Fig. 5·5, E) and vary [illegible] The wall is differentiated into three [illegible] nd variously sculptured. [illegible] tubercles (Fig. 5·15, E). [illegible] er wall is called **exos-** [illegible] which is followed by **intine or endosporium.** According to some authors the original

cell wall that separates the spore tetrads develops, in each spore, into an outermost sculptured layer called the **epispore**. Later exine or exosporium, mesine or mesosporium and intine or endosporium develop. According to them the spore wall is four layered. The spore protoplasm shows a spongy structure and contains food reserves in the form of starch. The nucleus, in the mature spore, lies at its apex (Fig. 5·15, E).

(b) *The microspores.* They are smaller in size and vary from 20—45μ in diameter. The microspores are semilunar in shape when young but become kidney-shaped at maturity. The cytoplasm is thin and finely vacuolated. The nucleus lies on one side. The microspore wall is three-layered. The outermost layer or exine is marked with small densely packed spines (*Fig.* 5·16, E). They are usually ash coloured or brown.

GAMETOPHYTES

Heterospory leads to the formation of two types of gametophytes in *Isoetes.* The microspores germinate to give rise to the male or

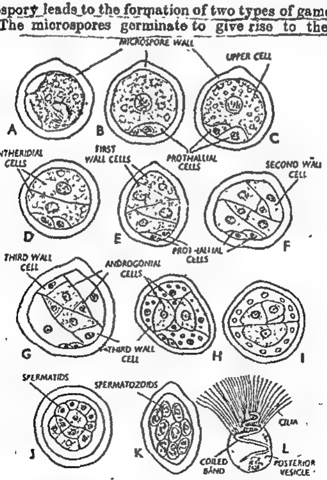


Fig. 5·17. Isoetes lacustris.
Various stages in microspore germination and formation of male gametophyte. For explanation see text. (After Liebig)

microgametophytes and the megaspores to female or **megagametophytes.** Both types of gametophytes are endosporic. The spores may start germinating immediately after their release from the sporangia or the germination may be delayed depending upon the climatic conditions. Quite contrary to *Selaginella* the spores in *Isoetes* start germinating only after their release from the sporangia. The germination is not **precocious.**

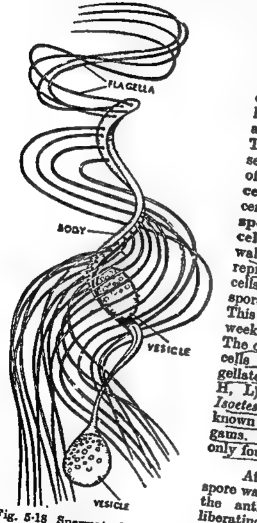


Fig. 5·18 Spermatozoid of Isoetes.

Microgametophyte. Numerous bean shaped microspores are set free by the decay of the microsporangial wall. The first division of the nucleus results in the formation of a small **Prothallial cell** and a large cell that has been interpreted as **antheridial initial** (Fig. 5·17, B). The antheridial cell undergoes a series of successive divisions to cut off 4 **wall cells** surrounding a single **central cell** (Fig. 5·17; C—G). The central cell divides twice to form four **spermatocytes** or **sperm mother cells** (Fig. 5·17, H—J). The four wall cells enclosing 4 spermatocytes represent the antheridium. The wall cells remain intact until the microspore wall cracks (Fig 5·17, N). This generally happens after two weeks of developmental period. The contents of the sperm mother cells metamorphose into multiflagellate spermatozoids (Fig. 5·17, H, L). The microgametophyte of *Isoetes* is the most reduced type known among the vascular cryptogams. One gametophyte produces only four spermatozoids.

After the cracking of microspore wall the exposed wall cells of the antheridium degenerate thus liberating the spermatozoids. The prothallial cell also degenerates. The multiflagellate sperms of *Isoetes* are in striking contrast to biflagellate sperms of other lycopods (*Selaginella, Lycopodium*).

The spermatozoid of *Isoetes* (Fig. 5·18) has been described by Dracinschi (1932). The free swimming spermatozoid consists of two large and spherical vesicles (Fig. 5.18). The vesicles are soon lost. Each vesicle contains fat and vacuole elements. Starch is considered to be absent. The nucleus is pointed at either end and is enclosed within a spongy plasmatic structure. The nucleus does not extend

to the pointed anterior end of spermatozoid. The flagella bearing band or the **stalk** is homogeneous and bears about 25 flagella. The flagella arise from the **basal granules** situated on the stalk. Four basal granules are grouped together at the anterior end whereas the rest are scattered in a single row along the stalk.

Mega-gametophyte. (Fig. 5·19, A—D)

The large tetrahedral megaspore starts germinating after it is set free from the megasporangium. It has a large nucleus and dense cytoplasmic contents. It has no large central vacuole and the nucleus may be either at the upper and pointed end of the megaspore (*I. lithophila*) or at its base (*I. braunii*). The nucleus divides by free nuclear divisions until 30—50 free nuclei are formed. The nuclei migrate through the cytoplasm and get distributed along the periphery of the spore protoplast. The larger number is near the apex (triradiate ridge). Wall formation starts after 30—50 free nucleate stage. The nuclei at the apical portion of the spore are quite close to each other and are the first to be surrounded by walls. From herewall for mation extends basipetally and then towards the centre at a comparatively slower rate. The whole megaspore is ultimately filled with cells. The cells at the apex are smaller in size and those lower down are larger in size and contain reserve food material. There is no diaphragm demarcating the upper small celled and lower large-celled tissue. This cellular tissue is the female gametophyte and is surrounded by the megaspore wall, which later cracks along the triradiate ridge thus exposing the upper small celled tissue (Fig. 5·19 A). The exposed part does not protrude out as in *Selaginella*. A number of rhizoids develop from the exposed part. Archegonia develop in the exposed small-celled tissue. The first archegonium appears at the apex and is thus median in position (Fig. 5·19). The number of archegonia varies ...

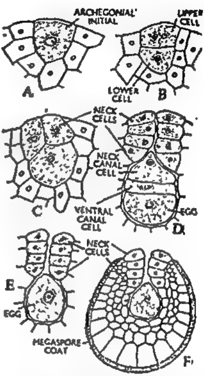


Fig. 5·19. **Isoetes echinospora.** A. Female gametophyte partly enclosed within the megaspore coat. A mature archegonium with egg is also shown. B. An archegonium in an earlier stage of development showing two tiers of neck cells, a neck canal cell, a ventral canal cell and an egg cell. C. A later stage of archegonium. D. Mature archegonium in which neck canal cell and ventral canal cell have disorganised. (After Campbell)

may not develop at all. Their formation stops after fertilization. In case fertilization is delayed the archegonia go on developing till the entire food supply is exhausted.

Archegonia

The archegonia are sunk in the tissue of the female gametophyte and only the upper tier of neck cells may protrude out slightly. [illegible] up of 4 longitudinal rows [illegible] neck canal cell. The venter has a **ventral canal cell** [illegible] egg [illegible] embedded the venter has no sterile jacket. At maturity the neck canal cell and ventral canal cell disintegrate and push apart the neck cells thus making an open channel for the spermatozoids to enter.

The archegonium develops (Fig. 5·19 B, D) from a single superficial cell which divides periclinally *into an upper and a lower cell.* The outer divides anticlinally and periclinally *to form* four tiers of four cells constituting the neck. The lower divides periclinally to form a **neck canal cell** and a **Primary ventral cell.** The latter divides into a **ventral canal cell** and an **egg cell.**

Fertilisation has not been observed in *Isoetes* but it takes place.

The Embryo

The fertilised ovum in *Isoetes* is quite conspicuous and almost fills the cavity of the venter. The fertilised egg divides by a *transverse or oblique transverse wall (Fig. 5·20 B). Both the cells* take part in the formation of the embryo and no suspensor is formed. The cell towards the neck of the archegonium can be regarded as the **hypobasal cell** and the one away from the neck as the **epibasal**

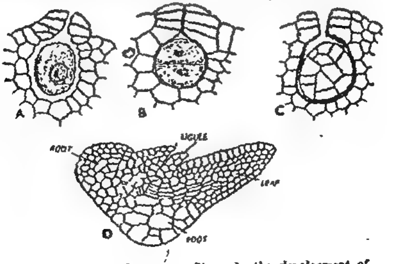


Fig. 5·20. **Isoetes echinospora.** *Stages in the development of embryo. (After Campbell)*

cell. The next two divisions are at right angles to the first wall and to each other thus forming an **octant stage.** The hypobasal tier of the octants gives rise to the foot alone. The epibasal tier gives rise to the first leaf and the root and also the shoot apex after some delay. Due to the absence of suspensor the development of … developmental changes suggest it … further development forms an … Later divisions lead to the widening of the embryo in the plane of the basal wall (Fig. 5·20 D). Later the first leaf originates from one half of the epibasal region (Fig. 5·20 D). From the base of the first leaf a large cell becomes prominent and divides first by periclinal walls to distinguish a ligule. A semicircular ridge appears at the same time at the base of the root. This is the primordium of the **velum.** Between the base of the velum and the first leaf there is a small cleft. In this cleft there distinguishes a small group of cells. This group of meristematic cells is destined to give rise to the shoot apex at a later stage. Unlike … is made up of a … Hegelmaier, 1872, … f develops facing the first with the shoot apex lying between them. Campbell (1918, 1939) observed that the vascular strands of the first leaf and the first root coincide with each other. The foot is small in young embryo but it becomes massive and well developed in mature embryos. During its growth, the embryo elongates downwards and erodes the prothallial tissue. The uneven growth of the embryo makes it curved and as this growth continues, accompanied by rapid absor-

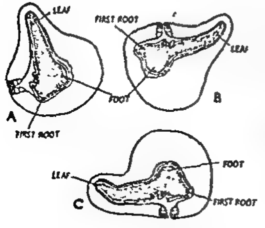


Fig. 5·21. Embryogeny in differently oriented gametophytes of Isoetes (After La Motte).

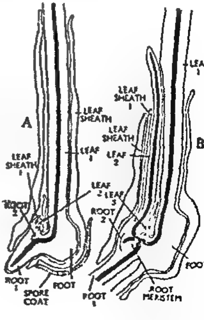


Fig. 5·22. Isoetes engelmanni (A—B.) L. S. Young. (After Baldwin)

ption of prothallial tissue, the polarity of the embryo becomes *reverse*. The foot which in the young embryo is towards the archegonial neck, comes to lie on the lower side (Fig. 5·20 D) and the long axis of the embryo lies parallel to the surface of the prothallus (Fig. 5 20 D). The young leaf elongates rapidly and in a horizontal direction. It comes out of the prothallus in horizontal position and later turns up. The root curves downwards and as the sporophyte grows it straightens out and all its traces of horizontal position are lost. The foot develops and persists till the storage tissue of the gametophyte lasts. It perishes after the young sporophyte becomes independent. The first leaf bursts out of the prothallus after seven days of the growth of the embryo.

Systematic Position

Bower and many other investigators regard *Isoetes* as a member of the ligulate Lycopsida because :—

1. It has ligulate and microphyllous leaves and is heterosporous.

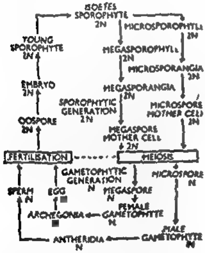


Fig. 5·23. Isoetes. Graphic representation of life cycle.

2. Germination of spores is similar to *Selaginella*.

3. Structure of male and female prothalli is also similar to *Selaginella*.

Campbell (1939) includes it under the eusporangiate fern because of the following features :—

1. Early leaf and root formation.

2. Delayed shoot formation.

3. Relationship of vascular strands of root and leaf.

These features bring *Isoetes* closer to *Botrychium virginianum* and to some Marattiaceae.

No secondary growth
Rhizophore
epiphytic
more spp
vessels present in xylem
Heterospory in sporophyte
embryo has two cotyledon
[illegible] well in dry condition

CHAPTER VI

LYCOPHYTA (contd.)

LIGULOPSIDA (contd.)

SELAGINELLALES

[illegible] living genus *Selaginella* included [illegible] enus *Selaginellites* was discovered [illegible] by *Selagnellites crassicinctus*, *S. primaevus*. Distinctive features [illegible]

(*i*) The sporophytes are herbaceous [illegible] of the species are dorsiventral; a few are [illegible] ure calle [illegible] (*v*) The [illegible] Presence [illegible] sporophy [illegible] e axils of sporophylls that are arranged in loose or compact strobili. (*x*) The micro and macrogametophytes are markedly different in size. (*xi*) The gametophytes are endosporic (*xii*) Spore germination [illegible] precocious. (*xiii*) The antherozoids are biflagellate. (*xiv*) The emryo has two cotyledons unlike other living lycopods.

SELAGINELLA

Distribution :—It is widely distributed genus with 700 species found under diverse climatic conditions. Majority of the species grow under shady and damp places especially in the tropical regions of the world. They are rare in the temperate regions and almost [illegible] hytic (*S. lepidophylla*). *S.* [illegible] ed as ornamentals due to [illegible] *S. pygmea*) *S. kraussiana*). Some of them form irridescent, bronze or bluish hues.

Senventy-one species of *Selaginella* grow in the tropical and subtropical forests along the Himalayas and in the plains of India. Some xerophytic Indian species include *S. Nightii*, *S. refanda*, etc. Majority of the species grow in the Eastern Himalayas (*S. biformis*, *S. adunca*, *S. monospora*, *S. caulescens* *S. ciliaris*, *S. intermedia*, etc.) and comparatively few in [illegible] *chrysocamlos*, *S. chrysorhizos*, *S.* [illegible] rows in Pachmahri hills (central In [illegible] are the extinct species reported from Sweden and Illinois.

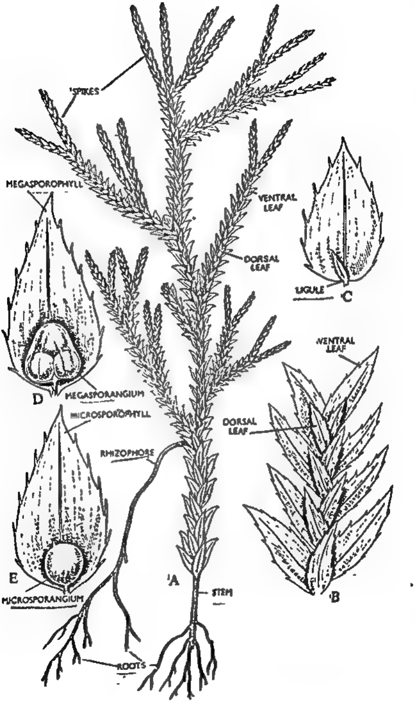


Fig. 6-1. *Selaginella chrysocaulos* (A—E).

A. Complete plant showing habit.
B. [illegible] shoot showing leaf arrangement.
C. [illegible] um.
D. [illegible] ium.
E. [illegible]

MORPHOLOGY OF THE SPOROPHYTE

Habit. Many species of *Selaginella* are herbaceous perennials, a few are annuals, *e.g. S. pygmaea*. Majority are dorsiventral and grow prostrate [illegible] *siana*, etc.) [illegible] *S. rupestri*[illegible] erect. So[illegible] caulescent [illegible] arising fro[illegible] a few centimetres (*S. pygmaea*) to a few metres (*S. pentagora*) in length and are capable of growing through and over the bushes (*S. wildenovii*). *S. alligans* is a climber and does so with the help of rhizophores that develop pad like discs at their ends. Some unbranched species are also known. The xerophytic species dry art and curl-like balls during dry seasons and again expand during favourable season or on welting with water.

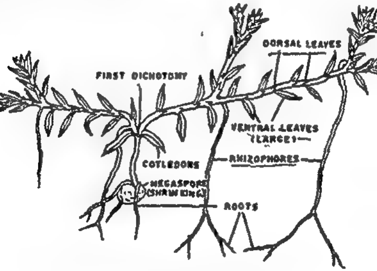


Fig. 6·2. *Selaginella kraussiana*. A young plant

Hieronymus (1902) divided the genus into two sections :

1: **Homoeophyllum** : This section includes about fifty species all of which have uniform or isophyllous leaves that are spirally arranged. They are all monostelic. This section is further divided into two sub-sections ;

(*a*) Sub section **Cylindrostachya** : It includes those isophyllous species in which the sporophylls are spirally arranged (Fig 5 5) *e. g., S. selaginoides* (=*S. spinosa*=*S. spinulosa*).

(*b*) Sub-section : **Tetragonostachya** : Species included in this section are isophyllous but the sporophylls are arranged in 4 vertical rows and give the strobilus a four-angled appearance *e g., S. pygmaea, S. uliginous, S. rupestris, S. oregana. etc.*

2. **Heterophyllum** : This section includes large number of species that are characterised by dorsiventral symmetry and by anisophylly (two kinds of leaves) The leaves are [illegible]

Oligomacrosporanglate, on the number of megasporophylls in the cone. The common species included in this section are *S. chrysocaulos*, *S. chrysorhizos*, *S. martensii*, *S. kraussiana* etc.

Stem. The stem is herbaceous, branched (rarely unbranched), solid, and may be prostrate, sub-erect, caulesent, climbing or erect. The erect species *S. selaginoides S. rupestris*, *S. pygmaea*) are radially constructed and belong to the section **Homoeophyllum**. The rest are all dorsiventral and are included under the section **Heterophyllum** (*S. chrysocaulos*, *S. chrysorrhizos*, *S. pallidissima*, *S. kraussiana*, etc.). Stem is usually green, smooth and glabrous, but it may be coloured red (*S. umbrosa*, *S haematoides*) and bear unicellular hair (*S. braunii*, *S. vogelii*). It is also articulated in some North American species.

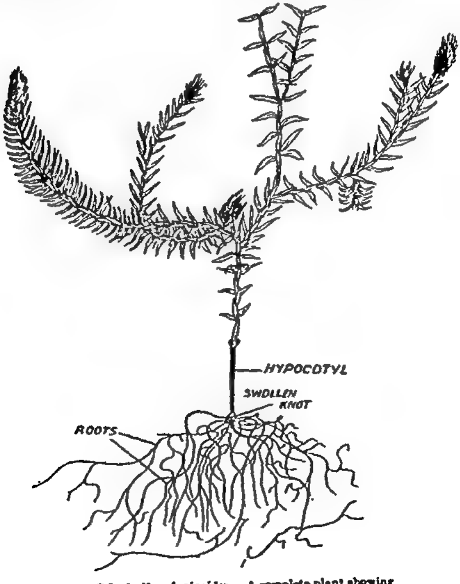


Fig. 6·3. *Selaginella selaginoides*. A complete plant showing radial symmetry. (After Bower)

tes of
wards
surround the shoot apex. Later pairs of epicotylar leaves make
their appearance.
dichotomously int
phyllous leaves.
dichotomously and
podial lateral branches arise in one plane and are at right angles to the first dichotomy thus giving the entire shoot a fan-like appearance. Strobili develop at the tips of stronger branches, whereas the rest remain sterile. The main axis and the hypocotyl remain as permanent structures (Fig. 6·3). The lower base of the hypocotyl swells up and gives out roots. The entire plant of *S. selaginoides*, therefore, has a central source of water supply and depends upon it throughout its life.

In the common and widely distributed *S. chrysocaulos* the prostrate and dorsiventral stem (*Fig.* 6·1, A) is repeatedly branched. The branching appears to be dichotomous in the younger portions of the stem and monopodial or lateral in the older portions. Smith, Scot and others hold that all the branches are really lateral but they appear to be dichotomous because they are formed so near the growing apex that the latter seems to give rise to two equal shoots. These shoots in the early formed portions of the plant grow with equal vigour so that it becomes difficult to distinguish between the main axis and the lateral branch. The equal growth of the main axis and the branch give the appearance of a dichotomy. The difference between the main axis and the branches becomes evident in later formed parts of the plant where the main axis grows vigorously and the branches remain small. Eames, Schoute, and others hold that branching in dorsiventral species of *Selaginella* is dichotomous or pseudomonopodial.

Leaves. [illegible]

hairy in *S.* [illegible]
leaf colour occurs in *S. serpens*.

The leaves are sessile and may be ovate, linear, lanceolate or cordate. Abnormal pinnalifid leaves have been reported in *S. lyallii* (Bruchmann, 1909).

There are about fifty species of *Selaginella* in which the leaves [illegible] is called **isophylly** [illegible] They are included [illegible] majority of [illegible] such a

called **anisophylly** and the leaves are called **anisophyllous** or dimorphic. These species are grouped under the section **Heterophyllum**.

The phyllotaxy or the arrangement of the leaves on the stem is always spiral in the isophyllous selaginellas (Fig. 6·3).

In the anisophyllous selaginellas (Heterophyllum), e g, *S. chrysocaulos* (Fig. 6·1, A), the small and large leaves form four longitudinal rows. The smaller leaves are arranged in two rows along the dorsal side of the stem. The larger leaves on the ventral side have their dorsal side turned towards the sky, whereas the small dorsal leaves have their ventral side facing the sky. The phyllotaxy is essentially decussate in all the dorsiventral selaginellas. A large ventral leaf is always opposite the small dorsal leaf so that the leaf pairs are unequal.

Ligule. The ligule develops quite early during the ontogeny of the leaf and arises from its base on the upper side. It varies in shape in different species of the genus. The ligule may be tongue shaped (*S. chrysocaulos*), wedge shaped (*S. Martensii*), lobed (*S. caulescens*), lanceolate or may even have fringed margins (*S. auspidata*). A mature ligule has a prominent basal portion called the **glossopodium** (Fig 6·10, F). It is surrounded by a sheath of specialised or unspecialised cells that are continuous with the epidermis of the leaf. In *S. rupestris* the cells of sheath possess **casparian strips** (Dunlop, 1949). The **glossopodium** is sunk in a definite ligular pit or pocket. Its function is not well understood. According to a number of workers the ligule is a secretory structure, which secretes or exudes water and sometimes mucilage and keeps the sporangium and the young leaf moist. The ligules during their development overgrow the leaf primordium and may be regarded as protective structures. They also overgrow the young sporangium.

Rhizophore. It is a structure of controversial morphological nature and present in most of the dorsiventral selaginellas. They are leafless and positively geotropic organs that have usually a localised origin and develop from the **angle meristems**, which are groups of meristematic cells present between the two branches of the stem. In majority of species only one rhizophore arises from such a meristem but in *S. martensii* two rhizophores arise from such a meristem. One of them is ventral in position and the other dorsal. The former remains short whereas the ventral one grows down into the soil and bears roots at its swollen end. In the climbing species the tips of rhizophores develop pad like thickening and help in climbing.

In *S. selaginoides* and other radial species the rhizophores are absent. In *S. selaginoides* are roots arise from the swollen base of the hypocotyl (Fig. 6 3).

Morphology of the rhizophore. Three different types of [illegible] have been advanced to solve the mor[illegible] [illegible]rding to one view they have [illegible] adventitious roots (Pfeffer,

Treub, Bruchmann, ... [illegible] The sup-
porters of the seco[illegible] ... [illegible]egham, Uphoff)
regard them as roots ... rhizophores as
organs *sui generis* (neither roots nor shoots).

The rhizophores are regarded as root-like structures due to the following characters :

1. They are positively geotropic.

2. They bear no leaves.

3. Their internal structure resembles that of a root.

4. Their stelar organisation is always monostelic even if the stems are polystelic.

[illegible]

tip of the rhizophore divides to form roots, and the older belief that roots arise endogenously from tip of rhizophore is not valid. These observations rule out any difference between the root and the rhizophore. Exogenous roots are also known in some Angiosperms.

The stem like characteristics of rhizophores are :

1. Their exogenous origin (roots of some angiosperms, *e.g.*, *Nasturtium austriacum* arise exogenously from the stem).

2. They develop from special meristems called the angle meristems that are present between the two branches of the stem.

3. They lack root caps (capless roots are also known).

4. They have no root hair.

5. Experimental evidence that under certain experimental conditions the rhizophores develop into leaf bearing shoots.

J. C. Schoute (1938) regards them as stems with root bearing functions because they lack root caps and root hair and are exogenous in origin. Regarding its anatomy Schoute points out that it is like stem in its organisation.

It has been [illegible] demonstrated by Bruchmann (1905) ... (1931, 1937) in *S. grandis* and *S.* ... [illegible]ative activity by inducing strobili formation or by decapitating leaf bearing shoots, the rhizophore rudiments can be made to grow into leafy shoots. Cusik (1954) concluded that some hormones produced by shoot apex induce angle meristems to grow into rhizophores. He proved it experimentally.

After [illegible] and others did not decide to [illegible] shoots but agreed with Bower [illegible] *sui generis*. The term organ [illegible] in this case implies that rhizophores

neither roots nor stems but are intermediate structures. According [illegible] is a novelty and has [illegible] organ. He disagrees [illegible] and others in treating rhizophores as structures *sui generis* because they are not novel structures and possess features in common with both the stems and the roots.

Roots. The roots are adventitious and originate from the (*i*) tips of rhizophores, (*ii*) from the swollen bases of hypocotyl and (*iii*) directly from the stem. They arise endogenously and branch dichotomously. In *S. chrysocaulos* (Fig. 6·3) and other dorsiventral species they arise from the swollen tips of the rhizophores. In *S. selaginoides* they arise from the swollen bases of the hypocotyl (Fig. 6·5). In *S. umbrosa*, *S. braunii*, etc., they arise directly from the stem and have no relation to the branching *i.e.*, they can arise from anywhere all along the stem. In some cases the roots arise only from the places where the stems branch, *e.g.*, *S. densa*.

The roots have root caps and bear root hair. The apical cell of the root cuts off some segments at its outer face. The segments contribute to the development of the root cap. In *S. selaginoides* an endophytic fungus has been reported in the cortical cells of the root.

ORGANIZATION OF THE STROBILUS

[illegible] the sp[illegible] sporop[illegible] may d[illegible] *ginella* [illegible] microsporangia [illegible] megasporangia [illegible] sporop[illegible] microsporo-phylls and those bearing megasporangia as megasporophylls. There is no morphological or anatomical differentiation between the micro and the megasporophylls. The microsporangia produce numerous [illegible] mega-[illegible] llus is [illegible] of an [illegible] in the [illegible] axis of the strobilus [illegible] strobilus to f[illegible] *S. erythropus* [illegible] again bears [illegible] in the formation of two strobilii on the same branch.

In *Selaginella selaginoides* the strobilus is cylindrical. The sporophylls are spirall[illegible] It is clearly marked off from the [illegible] sporangia have also been found to [illegible] vegetative leaves. In a large number of species the strobilus is tetragonous or four a[illegible] may be [illegible] decus-sisophy[illegible] vege-ate. [illegible]

tative region as well as the strobili (tetragonous) are anisophyllous. In all the cases [illegible] is present [illegible] Fig. 6·8).

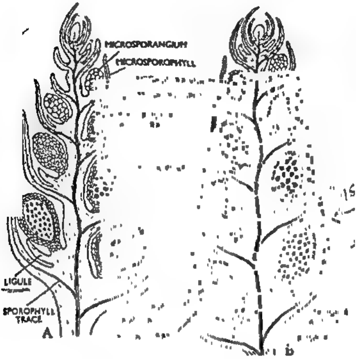


Fig. 6·4. (A—B). V.S. sporangiferous spikes of *Selaginella*. A. *S. Kraussiana*. B. *S. oregana*.

The strobilus [illegible] sporangiferous spike [illegible] **cone.** [illegible] or a [illegible] bispor [illegible] axils [illegible] The [illegible] and th [illegible] In *S.* [illegible] and many others the megasporophylls are restricted to the base of the strobilus and the microsporophylls to the upper region. In *S. caulescens* and *S. martensii* the two kinds of sporophylls are indiscriminately mingled along the entire length of the strobilus. In *S. kraussiana* (Fig. 6·4, A) there is only one megasporophyll at the base of the strobilus and the rest are all microsporophylls. In *S. oregana* (Fig. 6·4, B) the tetragonous strobilus has two rows of microsporophylls on one side and two rows of megasporophylls on the other side (Fig. 6·9).

In *S. atroviridis* and *S. gracilis* the strobili are [illegible] *i.e.*, a strobilus either bears microsporangia or it bears only [illegible]porangia. Both the microsporangiate and megasporangiate [illegible] occur on the same plant.

ANATOMY

Stem. The vascular region or the *stelar system* in *Selaginella* exhibits considerable variation in the different species or even in different parts of the stem in the same species. Anatomy of *S. chrysocaulos* is given in detail. Variations in other species are, however, given in brief.

Selaginella chrysocaulos (Fig. 6·5). It is a dorsiventral *species* and transverse section of the stem reveals the following structure :—

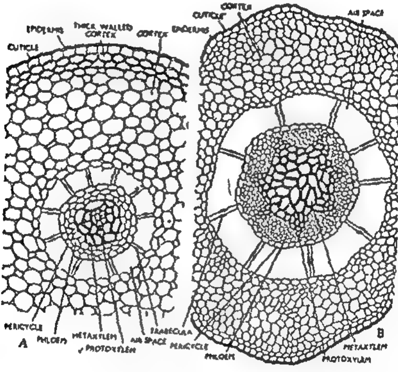


Fig. 6·5. Stem anatomy of *Selaginella selaginoides*.
[illegible] region of stem

Epidermis. It is made up of a single layer of cells. The cells are thin walled and rectangular or barrel-shaped. A thin layer of cuticle is evident as an outer protective coating. The cells are colourless and do not contain *chloroplasts*. There are no stomata in the epidermis.

Cortex. It lies below the epidermis and consists of many layers of cells. The outermost layers (usually 2·4) of cells develop *thick walls in the older regions* of stem and form **a sclerenchymatous hypodermis.** The rest of the cortex is made up of thin walled and polygonal cells. They enclose small intercellular spaces.

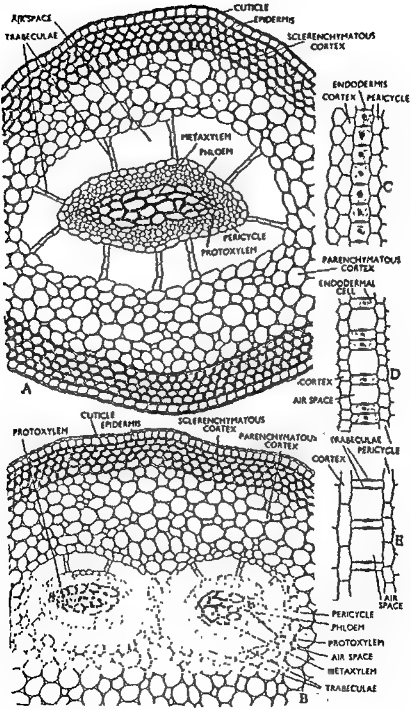


Fig. 66 (A—E). Anatomy of *Selaginella*.
A. T.S. stem of *S. chrysocaulos*
B. T.S. stem of *S. kraussiana*. Note distelic condition.
C—E. Development of trabeculae.

The thin walled cortical cells also contain chloroplasts. Sclerenchymatous hypodermis is absent in the younger parts of the stem.

Air space. Next to the cortex there is large air space in the centre of which lies the ste[illegible] by means of **trabeculae.** The trabeculae are modifie[illegible]s casparian strips (Fig. 6·6, A). These [illegible] of an endodermal layer. During the [illegible] 6·6, C—E) the endodermal cells elong[illegible]. As a result of this elongation the cells separate from each other (Fig. 6 6, D) and lead to the formation of air spaces. Further elongation results in the formation of a large air space traversed by elongated endodermal cells or the **trabeculae.** The trabeculae possess casparian strips. During the course of their radial elongation the trabeculae may divide and become two or more celled filaments.

Stele or the Vascular region. There is single central stele suspended in the air space by means of the trabeculae (Fig. 6·6, A). The stele in this species is flattened like a ribbon and is called a **protostele** because there is no pith in the centre. It consists of :—

(*a*) A single layer of thin walled cells called the **pericycle.** The pericycle completely encircles the inner vascular tissues.

(*b*) Next to the pericycle is **phloem.** The phloem consists of a layer of phloem parenchyma cells next to the pericycle and a layer or two of **sieve tubes.** The companion cells are absent. Phloem completely encircles the central xylem. The sieve cells appear as large polygonal cells in a cross section.

(*c*) The centre of the stele is occupied by the xylem tissue. The xylem, therefore, forms the core of the stele, there being no pith. The xylem consists of **metaxylem** and **protoxylem.** The metaxylem is composed of scalariform tracheids and xylem parenchyma cells. It forms the major portion of the flattened stele. The protoxylem occupies the two ends of the flattened metaxylem and is composed of annular and spiral tracheids. The xylem is, therefore, **exarch.** Since there are two groups of protoxylem at either end, the xylem is regarded as **diarch.** The xylem lacks vessels and fibres.

The protostele is **monostelic** because the stem has only one such stele. Other species with such a stele are *S. martensii*, *S. chrysorrhizos*, *S. flabellata*, etc.

In *S. selaginoides* (Fig. 6·5, A, B) a section of the stem from the upper region of the axis (Fig. 6 6, B) reveals an **actinostelic** (star-shaped) **protostele** with 7 groups of exarch protoxylem. A cross section through a portion of the stem in trailing region reveals a monostelic protostele with mesarch xylem (Fig. 6.6, A). In this case the protoxylem is in the centre and is surrounded on all sides by metaxylem (Fig. 6·6, A). In *S. kraussiana* there are two proto-

steles suspended in the air space. They are exarch. Such a stele is called distelic (Fig. 6·6, B).

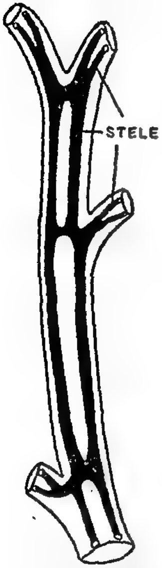


Fig. 6·7. *Selaginella kraussiana*. It shows longitudinal course of the two steles. They anastomose at the point of bifurcation of the stem.

The entire stem is traversed by two parallel steles that join only at the point of branching of the stem (Fig. 6 7) and again separate. Metaxylem consists of scalariform tracheids, whereas protoxylem is composed of annular and spiral tracheids. Bierhorst (1960) and Zamora (1960) reported that the helics of spiral tracheids in this species are variously wound in different parts of the same tracheid. The xylem is encircled by phloem which in turn is surrounded by pericycle. The phloem consists of a single layer of sieve tubes and parenchyma cells. Esau (1953), and Cheadle and Gifford (1953) reported that the sieve cells have many sieve areas on their inclined end walls and lateral walls. *Selaginella sulcata*, *S. galeottei*, *S. willdenovii*, etc., belong to this catagory.

In *willdenovii* (Fig. 6·8) there are three or even four ribbon like protosteles. The xylem is exarch. There are two groups of protoxylem, one at either end, in the central stele whereas in the other two that lie on either side of it there [illegible]

the stem is monostelic and becomes tristelic in the middle region of the stem. In the upper parts it may be even tetra or polystelic. All these steles run parallel to each other and fuse only at the point of branching of the stem. At certian places the air space and the trabeculae may be absent and the pericycle is in direct contact with the inner cortex.

The xylem in *S. oregana*, *S. rupestris*, *S. rupicola*, *S. arizonica* and *S. densa* has distinct vessels. In *S. rupestris* and *S. lepidophylla* the air space is inconspicuous.

Rhizophore (Fig. 6·9). In a transverse section the rhizophore reveals the same tissue systems as that of stem. On the outside there is a single layered epidermis uninterrupted by stomata. The cells of this layer may be thick walled. The cortex is extensive and is usually distinguished into an outer thick walled or sclerenchymatous cortex and an inner thin walled or parenchymatous cortex. Last layer of the cortex is called the **endodermis** and is followed by a single layer of parenchymatous cells called the **pericycle**. The endodermis is not very clear.

The stele is typically a **protostele** and shows variations in its form and arrangement of protoxylem in the different species of *Selaginella*. In *S. martensii* (Fig. 6·9) the metaxylem occupies the centre and the protoxylem forms a group of smaller tracheids

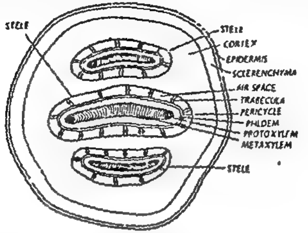


Fig. 6·8. T.S. (diagrammatic) stem of *S. Wildenovii* showing three protosteles.

on one side, *i.e.*, it is exarch. In *S. atroviridis* the metaxylem is half moon shaped or crescentic and the protoxylem occurs in the form of a few groups on the concave adaxial side. In *S. kraussiana* the condition is mesarch. The xylem is surrounded by phloem which consists of sieve cells and parenchyma.

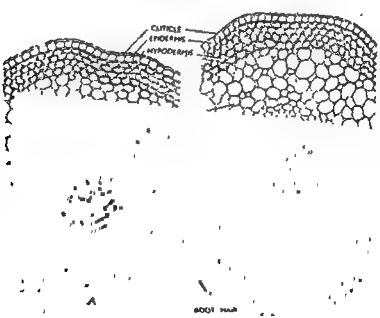


Fig. 6·9 (A—B). *Selaginella*. Anatomy of Root and *Rhizophore*. A. T.S. Rhizophore of *S. martensii*. B. T.S. Root of *S. chrysocaulos*.

Root. (Fig. 6 9, B). The root epidermis is single layered and is covered by a thin cuticle. Root hair are present.

The cortex is wide and extensive and usually consists of an outer sclerenchymatous cortex of 3 to [illegible] or more layers in thickness. Webster and Steeves (1963) described the entire cortex of older root in *S. densa* as sclerenchymatous. In the younger roots the sclerenchyma is peripheral in position and is followed by thin walled cortex. A distinct lacuna or air space has also been reported in the inner cortex of *S. densa* (Webster and Steeves, 1963). It is traversed by trabeculae that are not endodermal cells but cortical cells that elongate radially. This lacuna is absent in othes species.

The endodermis is usually indistinct but in some species it is distinguishable (*S. densa*, *S. rubella*, etc. Next to endodermis is a single layer of pericycle. The stele is typical **Protostele** with **exarch** and **monarch** xylem. There is only one group of protoxy-

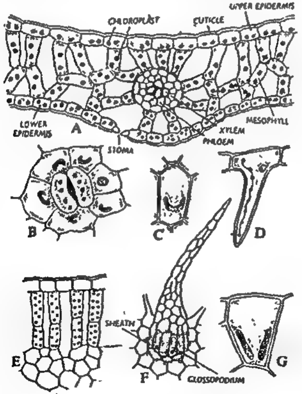


Fig. 6-10. *Selaginella*

A. V.S. leaf of *S. kraussiana*. B. A stoma from the living leaf of *S. martens*[illegible] *martensii* showing a single cup shap[illegible] living leaf of *S. martensii*. E. V.S. [illegible] net palisade and sp[illegible] tissue. F. A ligule. G. A mesophyll cell from the leaf of *S. caesia* sh[illegible] the two chloroplasts (B—D, after Emberger ; G, after Haberlandt ; after Harvey-Gibson).

lem that is peripheral in position. The phloem almost encircles the xylem except that opposite the protoxylem group the sieve tubes are absent or not properly developed.

Leaf. (Fig. 6·10). It is dorsiventral and consists of distinct upper and lower epidermises that are one cell in thickness. The stomata may be present on both the epidermal layers. In majority the species the stomata are restricted to the lower epidermis in the vicinity of the mid-rib. The epidermal cells contain chloroplasts and the cells composing the two epidermal layers may be similar in shape and size or they may show some differences. The cells in the upper epidermis of *S. martensii* are large and conical and those of the lower epidermis are comparatively smaller. In this species the stomata are restricted to the lower epidermis. The epidermal cells in some species bear hair like appendages.

The mesophyll is composed of thin walled cells that are loosely arranged and enclose small or large air spaces. In majority of the species it is made up of similar cells and is well developed in regions around the midrib and goes on diminishing towards the leaf margins where the epidermal layers are in contact and the mesophyll is absent. The mesophyll cells contain a variable number of chloroplasts and are the main seat of photosynthesis. The chloroplasts contain numerous spindle shaped bodies that ultimately become transformed into starch grains. They appear like the pyrenoids. The epidermal and mesophyll cells in *S. martensii* (Fig. 6·10, C) contain one cup shaped chloroplast. In *S. kraussiana* and *S. caesia* there are two and in *S. willdenovii* there are upto eight chloroplasts in each cell. Ultrastructural studies on the chloroplasts of *Selaginella* (McHale, 1965) reveal that they are intermediate between the algal chlorophyta and the spermatophyta. The chloroplasts show grana like structures called the 'granoids'. In *S. lyallii* (Fig. 6·10, E) and *S. concinna* the mesophyll *is distinguished into* a distinct palisade layer a spongy parenchyma.

The vascular bundle is very simple and traverses the leaf from base to the tip of the leaf or a little below it (*S. chrysocaulos*) and forms the mid rib. It has no branches and has a central xylem surrounded by a layer of phloem. The xylem has tracheids only and there is no distiction into proto and metaxylem. The tracheids may be annular or spiral. The phloem has a few sieve cells and a number of elongated parenchyma cells. A single layer of cells completely encircles the phloem. It may be regarded as the **bundle sheath.**

Ligule. The ligule arises from several short rows of superficial cells. A fully developed ligule consists of a distinct and hemispherical basal region where cells are large and thin walled and contain vacuolated cytoplasm. This region is the **glossopodium** (Fig. 6·10, F). It is surrounded by a sheath called the glossopodial sheath. In *S. kraussiana* and *S. rupestris* the sheath cells show *casparian strips*. The cells above the glossopodial region are large, polygonal and have densely granular cytoplasmic contens. The region is swollen and quite prominent. It is not surrounded by the

sheath. Next to this region the ligule usually (in many species) narrows down, or broadens or is produced into finger like processes. Depending upon the shape of the ligule the cells in the distal portion are likewise arranged. In the tongue shaped and spindle shaped ligules the cells in the distal region are narrow and elongated.

Apical Growth. Barclay (1931) studied the shoot apices of certain species of *Selaginella* and concluedd that there is an inter-

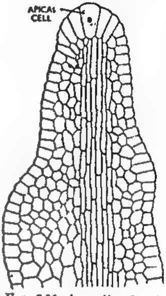


Fig. 6 11. A median longitudinal section through stem apex of *Selaginella* sp. showing a single apical cell.

cutting faces and the first segments thus cut off undergo periclinal divison to distinguish an outer layer that by further periclinal and acticlinal divisions gives rise to the epidermis and the cortex. The inner cells give rise to the endodermis, pericycle and the stele. In *S. selaginoides*, Bruchmann (1897) reported the apical growth to take place by a group of cells. Strasburger (1891) reported the occurrence of two apical cells in *S. wallichii* Williams (1931) reported two apical cells in *S. grandis*. The superficial cells very close to the stem apex give rise to the leaf primordia on either side of the apical region. During its early development procambial strands differentiate in the leaf and are connected with the vascular strand of the stem (Hsu, 1937). The procambial strands differentiate into primary xylem and phloem.

The rhizophore also ... the activity of a single ... its there is a single apical

Vegetative Propagation. Vegetative propagation in *Selaginella* is effected by the following methods :

Fragmentation. Fragmentation is not a common method of propagation. It is effected only in species that grow under humid conditions It has been reported in *S. rupestris*. In this case the trailing ... ious branches ... int and grow

Tubers. Formation of tubers has been reported in *S. chrysorrhizos* and *S. abyssinica*. In *S. chrysorrhizos* they are formed under...
The tubers bear ...

to perennate over the conditions of stress and strain. At the advent of favourable conditions the tubers rejuvenate and germinate to produce new sporophytes of *Selaginella*.

Resting buds (Fig. 6·12) have been reported to develop at the ends of some aerial branches in *S. chrysocaulos*. They develop at the close of the monsoon season and are very compact structures. The leaves in this region are closely arranged and overlap each other and cover the growing point (Fig. 6·12). The buds give off **rhizophores** that bear roots at their tips (Fig. 6·12) and fix them to the soil. The resting buds survive the unfavourable periods when the rest of the plant dies. They grow into new individuals at the return of favourable conditions. They serve the dual purpose of perennation and propagation.

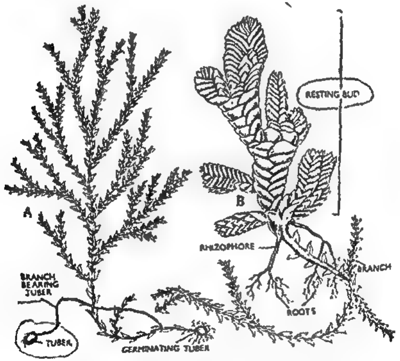


Fig. 6·12. Vegetative propagation in *Selaginella*.
A. Plant formed by the germination of a tuber. Also note that the same plant bears a new tuber at the tip of a specialised branch. This is in *S. chrysorrhizos*.
B. Portion of plant of *S. chrysocaulos* bearing a resting bud. (Highly enlarged).

Reproduction by Meiospores. *Selaginella* is heterosporous and the **meiospores** are of two kinds: (*i*) **micromeiospores** or **microspores**, and (*ii*) **megameiospores** or **megaspores**. They are produced in **microsporangia** and **megasporangia** as a result of meiosis of the spore mother cells. The two kinds of sporangia arise in the axils of **microsporophylls** and **megasporophylls** and may be **cauline** or **foliar** in nature. The sporophylls are

arranged in definite loose or compact and terminal structures called the **strobili** or **spikes**. They develop at a certain stage of maturity.

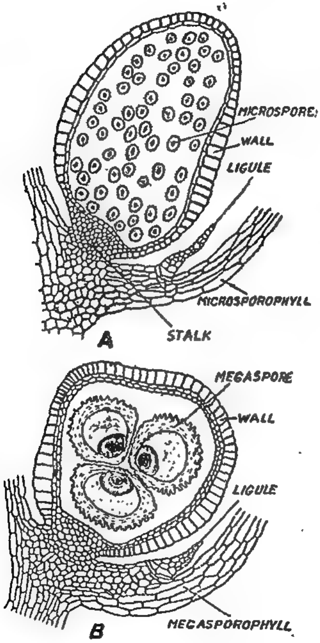


Fig. 6·13. *Selaginella apus*

A. A mature microsporangium with ligule and sporophyll.

B. A mature megasporangium showing three megaspores. (After Lyon)

The tapetum lies next to the inner layer of wall and is in direct

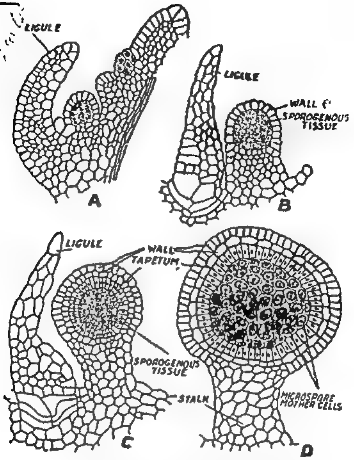


Fig. 6 13.
Development of microsporangium in *Selaginella galeottii* (After Haupt).

contact with the sporogenous cells. It persists till the spores are formed and its cells ma[illegible] divide repeatedly and t[illegible] **spore mother cells.** [illegible] mega-sporangia is simila[illegible] course.

In the microsporangia usually all the **microspore mother cells** are functional and undergo **meiosis** to form **tetrahedral tetrads** of microspores. These, later, separate into individual microspores. The tapetal cells now disorganise and form a continuous **plasmodial fluid** in which the microspores float and receive nourishment.

In *S. galeottii* a single transverse row of sporangial initials is [illegible]

an outer row of **jacket initials** and an inner row of **arches-**

porial cells (Fig. 6·13). The **jacket initials** undergo periclinal and anticlinal divisions to form a two layered wall of the sporangium (Fig. 6·13, C). The archesporial cells divide in all planes and give rise to a mass of **sporogenous cells** (Figs. 6·13 and 6·15).

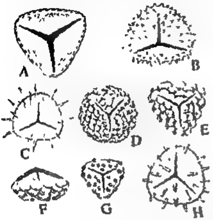


Fig. 6·14. Megaspore of various species of *Selaginella* illustrating spore coat morphology.

A. *S. repens* with granulose ectine. B. Spinose ectine in *S. galeittei*. C. Spinose ectine in *S. xiphophila*. D. Tuberculate ectine in *S. chrysocaulos*. E. Verrucate ectine in *S. mongolica*. F. same as E. G. Baculate ectine in *S. haematides*. H. Spinose ectine in *S. spinosa*.

(After Knox, 1931)

Brooks and Tepfer (1972) have experimentally shown that a sporangium is sexually uncommitted until just prior to the determination of functional and nonfunctional sporocytes, before meio-

porangia near base of strobilus and microsporangia at the apex. Similar results were obtained by treatment with ethylene as a spray.

Dehiscence. The mature microsporangium dehisces by the

the wall into two valves that separate. The basal region of the sporangium remains intact and appears boat-shaped. The cells of the wall in this region shrink due to the loss of water. The shrinking lower part exerts pressure on the spores within and forces them out with a little violence through the split upper part. The semigerminated micro-spores fall at a little distance that may be a few centimetres. All the microspores are not thrown out at once but they are expelled at intervals either by intermittent opening and closing of the split upper part of the sporangial wall, or if the sporangial split remains open the spores are scattered, in small masses, by the wind.

MEGASPORANGIA (Fig. 6·12)

Structure. It is comparatively larger in size than the micro- … At maturity the mega- … be corresponding in … lour it varies and … cies and white and … l and a third layer … spore mother cells … rs degenerate. The … m a tetrad of four … usually disorganises

(Fig. 6·12, B) but this is by no means true for all species. The megaspores separate and grow considerably in size so as to fill up the whole sporangium. The megasporangium becomes four lobed [illegible] pores. In some species [illegible] so that their number [illegible] spora and other species only one megaspore is left behind. In *S. willdenovii* the number of [illegible] 24 or even 36 or 40. The size of the [illegible] varies. In *S. molliceps* one megaspore [illegible] smaller in size. In *S. stenophylla* two megaspores are large and two small in size. In *S. caulescens* the megaspore has wing like extensions.

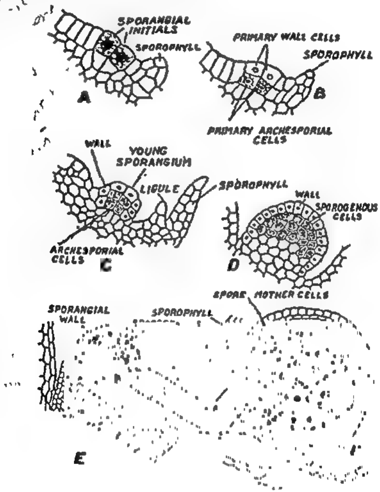


Fig. 6·15. (A—F). Various stages of development of sporangium in *Selaginella*.
A—C. *Selaginella martensii*.
D—F. *S. selaginoides*. (After Bower)

When fully mature the megasporangium has only one jacket layer whose walls become thick and radially elongated.

Development (Fig. 6·15). It is similar to microsporangium

up to the differentiation of spore mother cells. In case it is destined to become a megasporangium, only one *megaspore mother cell* remains functional and others [illegible] The functional megaspore undergoes meiosis to [illegible] The number of functional megaspore [illegible] nd to vary from one to ten. In majority of species only one megaspore mother cell is functional and produces 4 haploid megaspores. The number of megaspores in various species has been recorded to vary between 1 to 42. After the formation of tetrads there is sometimes abortion of the megaspores. This also leads to variations in the number of surviving megaspores. In *S. erythropus, S. monospora, S. rupestris* and *S. sulcata* there is only one megaspore in each sporangium.

James French (1972, 224-227) has observed that in *S. bigelovii* [illegible] microsporangia show growth differences before [illegible] cies the developing [illegible] and grows more vigorously before sporocyte [illegible] horst (1971) is also of the same opinion (*cf.* Brooks and Tepfey, 1972).

Dehiscence. It is similar to microsporangium. The megasporangia dehisce violently and scatter megaspores to a greater distance as compared to the microspores by the microsporangia. The megaspores start germinating in the megasporangium and are disseminated in a semi-germinated condition.

THE GAMETOPHYTIC GENERATION

The meiospores which germinate to give rise to the two types of endosporic gametophytes (Micro- and Mega-gametophytes are the pioneer structures of this generation. The two types of gametophytes are greatly reduced. Their structure and development are discussed below :

Microspores (Fig. 6·12, A) The microspores range in diameter from 0·015 mm. to 0·06 mm. They are usually tetrahedral in shape [illegible] upper end A triradiate mark is distinct. Every [illegible] toplasm that is enclosed [illegible] lled *exine* and is thick and variously [illegible] entiated into two layers ; (*i*) the outer **ectine** or **sexine** ; and (*ii*) an inner **endine** or **nexine**. The ectine is composed of radially arranged rods called the **columellae.** [illegible] are fused at their tips to form a layer [illegible] tegillum [illegible] tectum [illegible] variously sculptured. [illegible] s in various species of Selaginella [illegible]

also. The inner [illegible]
The intine contains cellulose an[illegible]
The cytoplasm contains reserve foo[illegible]
other fatty substances and even nitrogenous mat[illegible] little water and no chloroplasts. The exine contains **sporopollenin,** waxy substances and a variety of carbohydrates.

Microgametophyte (Fig. 6·16).

Microspore. A complete account of has been given by Slagg (1932) for t starts is a 13 stages of can be summarised as below :

The haploid nucleus of the microspore divides into two daughter nuclei. One of the two daughter nuclei migrates to one side of the spore. A cell wall is laid down separating a small, lens shaped **prothallial cell** from a larger **antheridial cell** (Fig. 6·16, B) This division is hal- not cell ives first by a vertical wall (Fig 6. 16, A, 2—2). The 6 16, 3—3) at right angles to the first plane of division This wall can be seen only if we cut a vertical section of the spore. This is the five-celled stage : one prothallial cell plus four antheridial cells. Out of the four cells thus formed two basal cells do not divide further. The upper two cells divide further by a curved wall that meets the second wall (2—2 somewhere in the middle (Fig. 16, A, 4—4). The microgametophyte has seven cells at this stage, *i e.*, 6+1. Out of the four cells formed by the last division the two bigger ones divide again by curved walls (Fig. 6 16, A, B, 5—5) and result in the formation of eight antheridial cells arranged in a manner that there are four cells in the middle quite separate from two cells on either side above and below. The middle four

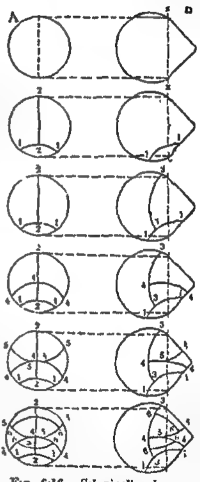


Fig. 6·16. *Selaginella kraussiana.* Development of Male gametophyte. In B the developing microspores have been shown in vertical sections. In A the spores are cut at right angles to those in A at the plane x—x.

(After Slagg).

t cells. 4 pri- stage The

rest of the development proceeds when they fall on a suitable substratum. There are, however, examples when the microgametophytes are liberated at an earlier stage. In this case they usually fall on the partially opened female gametophytes and proceed with further development in their close vicinity. In some species the ... re than ... phytes ...

During further development of the 13-celled stage only the four central **primary androgonial cells** divide. They give rise to 128—256 **androcytes** or antherozoid mother cells. During the formation of **androcytes** the eight jacket cells of the antheridium and the prothallial cell undergo degeneration so that the 256 ... in the mucilage filled ... this stage the androcytes ...

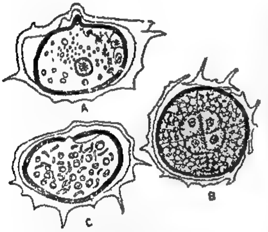


Fig. 6·17. *Selaginella kraussiana.* A T.S. spore showing a small prothallial cell. B. T.S. germinated spore showing 4 primary androgonial cells and jacket cells. C. T.S. mature male gametophyte containing spermatozoids. (After Slagg).

Spermatozoid. The cytoplasm of each androcyte metamorphoses into a biflagellate spermatozoid (Fig. 6·18, A—C). The spermatozoid of *Selaginella* has the usual three parts distinguished by Muhldor (1930), *viz.*, the **nucleus**, the **vesicle** (the plasma part) and the **motor apparatus** that consists of cilia bearing band or the **stalk** of the **motor** apparatus and the cilia. The ... tozoids have their body coiled around the lens shaped vesicle (Fig. 6·18, C). Later the vesicle absorbs water and becomes spherical and is soon set free.

The nucleus of the spermatozoid is rod shaped and is embedded in cytoplasm or the plasma part (Fig. 6·18, A, B). The stalk of the motor apparatus is located at the anterior end of the spermatozoid. It bears two flagella (Fig. 6·18, A—C). One of them is at the extreme tip and the other a little below (Fig 6·18, B). The former is smaller and the later longer. Each one of these cilia is attached ... Yuasa studied the spermatozoids of *S. in-* ... at the same point and one of ... atozoid for a certain distance ... of *Selaginella* resemble spermatozoids of *Lycopodium*, liverworts and *Chara*, in striking contrast to those of vascular cryptogams.

The male gametophyte of *Selaginella* is extermely reduced like that of *Isoetes*, but in this case the wall of the antheridium degenerates before the spore wall cracks open and the androcytes are lying free within the spore wall. In *Isoetes* the antheridial wall persist and degenerates only after the liberation of microgametophyte from the spore wall. In *Selaginella* there are 8 wall cells as compared to 4 in *Isoetes*. In *Isoetes* one antheridum produces only 4 multiflagellate spermatozoids. There is a greater reduction in the tissue of the microgametophyte in *Isoetes*.

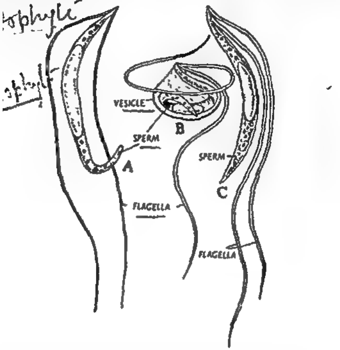


Fig. 6·18 (A—C).

A. Liberated sperm of *S involvens*. B. Liberated sperm of a species of *Selaginella*, in which vesicle has been dispensed with. C. A sperm with vesicle (A, after Yuasa; B—C, (after Dracinschi)

Morphology of Antheridium

Various morphological interpretatio [illegible] of male gametophyte [illegible] to conclude that the [illegible] there is no prothallial [illegible] number varies in s [illegible] in *S. kraussiana*, a [illegible] (1932) is also sup [illegible] Belajeff and Millardet.

Morphology of Prothallial Cell

The single prothallial cell of the microgametophyte [illegible] valent to the entire gametophytic tissue of the [illegible] gams, e.g., *Lycopodium*, *Equisetum*. [illegible] mann (1909) the eight jacket cells are also [illegible]

Megaspores (Figs. 6·14, A—H, 6·19). They range in diameter from one mill [illegible] hedral in shape. There is a [illegible] The megaspore is also u [illegible] is devoid of chloroplas [illegible] trogenous materials, w [illegible] are *enveloped by a two-layered thick wall.* The outer layer [illegible] and variously sculptured and called the **exine.** The exine is differentiated into two layers : (*i*) the outer heterogenous layer called the **ectine** (or sexine) ; and (*ii*) an inner homogenous layer called the **endine** (or nexine). The ectine is composed of radially arranged rods called the **columellae** that are fused *to form a layer called* **tegillum** or **tectum** which is variously sulptured. The endine is closely applied to the **intine.** The inner layer is thin and hyaline and is called the **intine.**

Megagametophytes. (Fig. 6·19). The megagametophytes develop as [illegible] of megaspores. The germination is precocious [illegible] sporangium, in majority of [illegible] *helvetica.* In these two species the megaspore germinates [illegible] ng shed. The species with precocious germination *release the semigerminated megaspores at* various stages. In *S. kraussiana* they are shed when the megagametophytes have produced the apical cellular cushion and first archegonium. In *S. apus* and *S. rupestris* the megagametophytes develop fully within the sporangia and are even fertilised *in situ* and develop embryo and young sporophytes before being liberated.

Campbell (1902) studied the development of megagametophyte in *S. kraussiana* and the following account *is based on his observations* (Fig. 6·19). The growing megaspores obtain nourishment from the tapetal fluid and start germinating. The first visible change is the separation *of* **endine** from the **ectine** *due to greater growth* of the latter. The space thus formed is filled with a nonstainable fluid. The intine is closely applied to the endine. The cytoplasm forms a thin lining layer *next to intine and* encloses a big vacuole with nucleus embedded in the cytoplasmic layer. Before the commencement of free nuclear division the cytoplasm contracts slightly from the intine and forms a globular vesicle. As a consequence of free nuclear division the number of *nuclei increases.* At first the nuclei are flattened but they become rounded with increase in amount of the cytoplasm. The nuclei are evenly distributed throughout the cytoplasm. Later the distribution becomes uneven and the number of nuclei increases towards the apex of the spore *and are* comparatively few towards the basal region. At this stage there is a big central vacuole and the cytoplasm increases in amount and again touches the intine. *Later due to the increased* nuclear division and consequent increase in cytoplasm the central vacuole *diminishes* in size. The cytoplasmic layer is comparatively thicker towards the apical region of spore.

The cell walls are laid down first around the nuclei in the apical region. Wall for[illegible] here is no wall towards the inner side [illegible] the walls are first laid down around [illegible] n the apical region so that a single layer of cells is formed. Later cell walls are laid down around the lower layers of nuclei forming three layers of cells in the middle and only a single layer towards the margins (Fig. 6·19). The innermost layer of cells is in contact with the vacuole. Later the inner walls of innermost cells become thickened thus forming a diaphragm. The diaphragm separates [illegible] the b[illegible] wall [illegible] remarkable degree the endosperm formation in seed plants. The diaphragm is not formed in all the species.

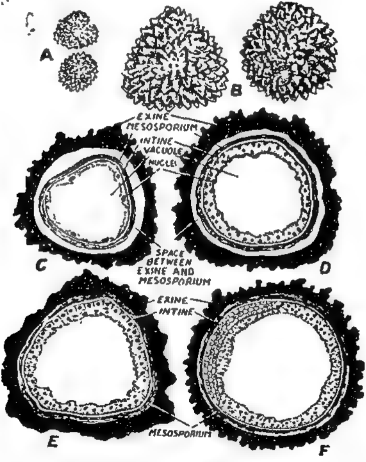


Fig 6·19 (A—F). A. Microspores of *S. chrysocaulos* B. Megaspores of *S. chrysocaulos*. C—F. Stages in the germination of megaspore in *S. kraussiana* (C—F after Campbell)

The free nuclei in the lower region continue to divide [illegible] amount of cytoplasm increases till the [illegible] obliterated. The cell walls in this [illegible]

in different species. In *S. kraussiana* this region becomes cellular after the development of
region. In some other
fertilisation or during
large in size and store
and starches. It provides nourishment to the developing embryo and has been termed as **secondary endosperm** by Pfeffer.

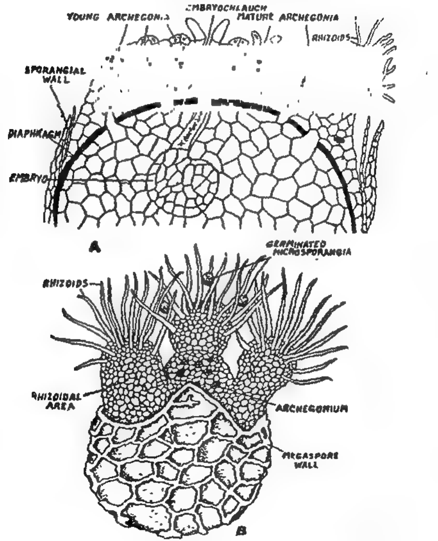


Fig. 6·20 (A, B).

A. Median longitudinal section through mature female gametophyte of *S. kraussiana* showing the upper cushion with archegonia and rhizoids. Also note the diaphragm and the lower tissue.
B. Megametophyte of *S. galeottii* showing rhizoidal mounds.
(After Bruchmann)

The entire megagametophyte becomes cellular at one or the

1. Upper cushion of small cells or the generative region. The

The megagametophytes in *S. kraussiana* are released at this

re.

In *S. galeottii* distinct mounds of tissue develop on the exposed region (Fig 6 20) surround the cent these mounds h within them and

D The archegonia are produc and are not formed in any usually occupy the central position on the apical cushion and are surrounded by the rhizoids. Each archegonium

initial (Fig. 6·21, A). It divides by a periclinal wall to form an **upper primary cover cell** and a lower central cell (Fig. 6 21, B). The central

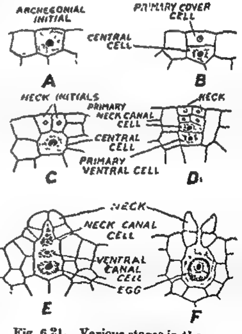


Fig. 6 21. Various stages in the development of an archegonium in *S. kraussiana*
(After Bruchmann)

canal cell does not divide further and acts as a single **neck canal cell**. The primary ventral cell undergoes periclinal division to form a **ventral canal cell** and an egg cell. The former lies below neck canal cell. The neck canal cell, the ventral canal cell and the egg cell form an axial row of cells in the archegonium. When all these changes are going on, the primary cover cell divides into four **neck initials** by two

vertically intersecting walls (Fig. 6·21, C). Each neck initial divides by a transverse wall to form eight celled neck (Fig. 6·21, D) of the ... four cells ... re arche- ... he apical cushion of the megagametophyte.

The mature archegonium (Figs. 6·21, E and 6·22) consists of a distinct neck composed of two tiers of four cells each, the upper tier functioning as cover cells The neck encloses a single neck canal cell. The venter portion consists of a single ventral canal cell and an egg. The venter is not surrounded by any definite venter wall because the archegonium is embedded in the tissue of the gametophyte The only projecting portion is the upper tier of neck cells.

The neck canal cell and the ventral canal cell disintegrate at maturity and form a mucilage that absorbs water and swells up to force apart the four cover cells. This leads to the formation of an open canal for the spermatozoids to swim down to the egg (Fig. 6·21, F).

Fertilization. It is effected by any one of the following methods :

In some species the megagametophyte falls on moist soil and the microgametophyte enclosed within the spore wall happens to fall

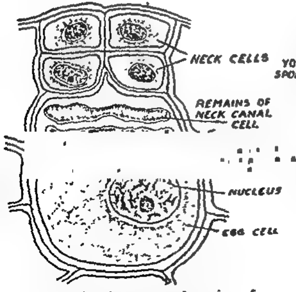


Fig. 6·22. A mature archegonium of *Selaginella kraussiana* as seen under electron microscope (after Bell and Woodcock)

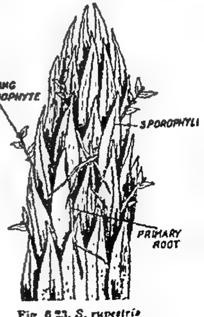


Fig. 6·23. *S. rupestris* The young sporophytes have developed upon the strobilus of the parent plant. (After Lyon)

on it or gets entangled in the rhizoid tuft (*S. galeottii*) and discharges the spermatozoids directly over the archegonial surface. The spermatozoids swim in dew drops or rain water and reach the open archegonial necks, the source of attraction being malic acid present in the mucilage that oozes out of the open archegonial necks. More than one sperms may swim down the canal but only one penetrates the egg to accomplish fertilization. The fertilised egg secretes a wall around it to become **a zygote or the oospore.**

In *S. rupest*

archegonia. The microgameto-
upon the open megasporangium,
their wall bursts open and liberates the spermatozoids that enter the megasporangium and reach the exposed archegonial surface of the contained megagametophyte and effect fertilisation. In these

Parthenogenesis

nomenon where the egg develops into embryo without the act of fertilisation is called **parthenogenesis.**

direct
develc

The Embryo

The zygote is the pioneer structure of the sporophyte generation and as a consequence of a series of orderly changes develops into an embryo. The embryology in *Selaginella* varies slightly with species. We shall consider in detail the embryology of *S. martensii*.

Embryology in Selaginella martensii (Fig. 6·24). The

two equal cells by a vertical wall. (II—II). A second vertical wall at right angles to the first (Bruchmann, 1909) leads to the
of four cells (only two are visible in one section) or the

stage. One of the four cells divides by an oblique wall (III—III) resulting in the formation of the shoot apical cell (Fig. 6·24, B). The remaining four cells (3+1) divide by transverse walls to form eight cells arranged in two tiers of four cells each. The cells in both the tiers divide by vertical and transverse walls forming an undifferentiated mass of cells (Fig. 6·24 C). The cell divisions are more [illegible] nearer the suspensor and form a distinct [illegible] 6·24, F). Greater growth in the foot [illegible] e embryonal mass at right angles to [illegible] Two superficial cells in two diagon[illegible] nts away from suspensor) differen[illegible] ons (Fig. 6·24, D, E) They are on [illegible] al. The cotyledon initials, by their division, give rise to two cotyledons each of which develops a ligule near to its base [illegible] hile the apical cell of the stem has divided to [illegible] sed by the cotyledons. The cells poste... [illegible] shoot apex give rise to the hypocotyl.

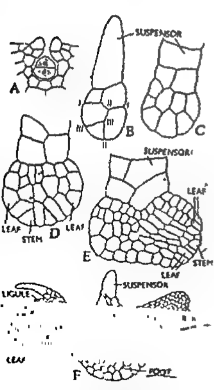


Fig. 6 [illegible] Embryo development in *S. martensii.*

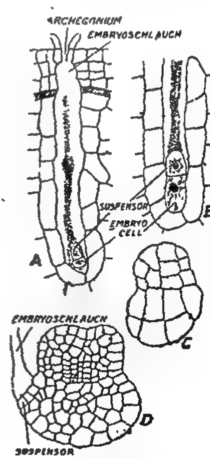


Fig. 6·25. *Selaginella krausiana.* Stages in the development of embryo. (After Bruchmann)

The root initial differentiates quite late in the development of the embryo.
the suspensor
species differer
F). The root apical cell cuts off segments and give rise to a structure

ed for some time. The vascular elements or the stele appears first in the stem as narrow and elongated cells called the procambial strands. These cells differentiate into xylem and phloem elements. Later the stele extends into the rhizophore and the root.

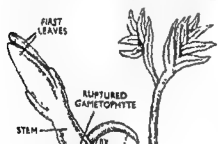
In *S. kraussiana* the peculiar feature is the enlargement and cavity deep into the gametophytic appears as a long tubular structure **embryoschlauch.**' The two-celled embryo lies at the tip of the **embryoschlauch** where it undergoes further division. The embryonal cell gives rise to stem apex, leaf apices and hypocotyl. The foot, root and suspensor develop from the suspensor cell. Root initial appears quite late between the foot and the suspensor. The suspensor is not well developed and is single-celled because its function is performed by the **embryoschlauch.** Embryoschlauch also develops in *S. rubicaulis* and *S. galeottei* but in this case the embryonal cell gives rise only to shoot apex and leaf initials, the root, foot and hypocotyl develop from suspensor cells. In these cases the first wall of the zygote is obliquely vertical and not transverse.

HETEROSPORY

Introduction—Heterossory is a condition that interprets the produ
ments
spores microspores
termed as **megaspores.**
terns because th
microgametophytes
megagametophytes
microsporangia and the megaspores is **megasporangia.** The microspores are produced in large numbers and are smaller in size as compared to megaspores that are produced in comparatively much smaller number and are

large in size. The larger size of the megaspores is attributed to the availability of more nutrients. They are few in number per megasporangium and get more nutrition, as compared to many microspores per microsporangiu
has been achieved
mother cells, or by

Importance of Heterospory :—The most important aspect of heterospory is that it is an expression of sex determining process of the plant It has brought about, along with its onset, a phenomenal shift of sex determining capacity from the gametophyte to the sporophyte. In all the homosporous individuals the sex determinants exert their effect in the gametophytes during the formation of the antheridia and



mother cells. differences start. In the microsporangia all the spore mother cells are functional and produce

Fig.

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alo

me, their endosporic nature
partial and ultimately com-
and female gametophyte on
nber of megaspores to one;
mets, and ultimately loss of
giosperms and organic union

between the ... ıgium. All these new ·hanges have gradually ... abit

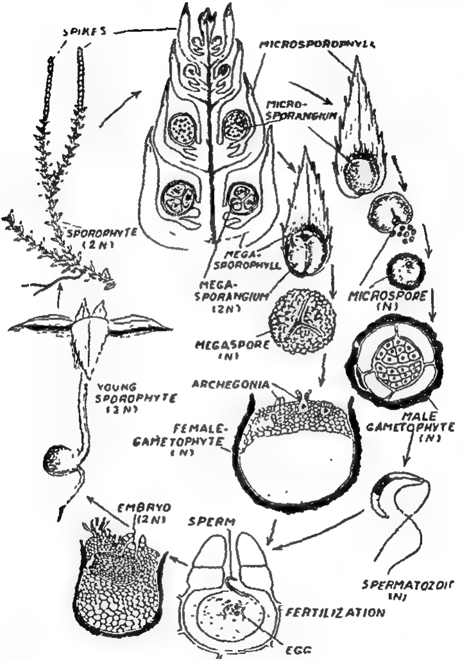

Fig. 6 27. Selaginella.
A diagrammatic representation of the life cycle.

Origin of Heterospory. The heterospory can be better discussed if we examine evidences from **palaeobotany**, from **developmental studies** and from the **experimental results.**

(a) Evidence from Palaeobotany. The available fossil record suggests that there was an early and widespread occurrence of heterospory in almost all the major plant groups. A number of heterosporous genera belonging to the **Lycopsida**, **Sphenopsida** and **Pteropsida** were known in the late Devonian and early Carboniferous periods. Some of them exhibit stages where heterospory is not pronounced whereas in others heterospory was well developed and approached the seed condition. These various grades of heterospory in these early land plants advance strong suggestions as to the origin of the heterosporous condition. Williamson and Scott (1894) discovered and described two species of **Calamostachys** (**Sphenopsida**) *that indicate the initial steps that might have led to heterospory. These species are C. binneyana and C. casheana.* The former species is homosporous but in some sporangia there were a few spores of unequal sizes. *C. casheana* showed distinct heterospory as there were microspores and megaspores produced in separate sporangia. The megaspor-

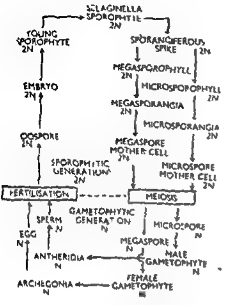

Fig. 6 28. Graphic life cycle of *Selaginella*.

spores leads to the differences in size ... *Sphenophyllum dawsoni* (Sphenopsida), ... homosporous. Thoday found that some sporangia in this species showed abortion of some spore tetrads and the remaining spores grew larger in size than the spores usual for the species. In *Stauropteris burntislandica*, Chaloner (1958) reported that the megasporangia contained tetrads of megaspores in which two spores were large and two small. This is also a case of reduction in the number of megaspores due to abortion. Scott (1901) reported that in *Lepidocarpon* (Lycopsida) three megaspores out of each tetrad had aborted and only one matured. In *Lepidostrobus braidwoodensis*, Arnold (1938) reported that the megasporangia contained only one mature megaspore in addition to a number of aborted spores. In *Miadesmia* (Arnold, 1938) the seed like megasporangia contained only one megaspore and there was no trace of aborted spores. These examples give us an idea of the reduction in the number of spores and differences in their sizes but whether it was achieved through abortion of the spores or through reduction in the number of spore mother cells, cannot be determined as there is no information regarding the development of the sporangia and the spores. We have no developmental record to show that these spores produced *heterothallic gametophytes*. *In the absence of such an information, it is not possible to shed light on the importance of the difference in the size of the spores, and whether these spores* a ... Baxter (1972) discovered ... Kansas ... appeared ... sporangium has one megaspore and is attached to the lower surface of the pinnule. A marginal indusium covers the sporangia partially. The megaspore completely fills the sporangium.

(b) Developmental Evidence The living representatives of the *major* divisions of the vascular cryptogams (Lycopsida, Sphenopsida, *Pteropsida*) include a number of heterosporous *genera* (*Selaginella*, *Isoetes*, *Marsilea*, *Pilularia*, *Regnellidium*, *Salvinia*, *Azolla* and *Stylites*). They afford us the

possibilities of extensive morphological, developmental and comparative studies that can throw much light on the origin of heterosporous condition in the plants. The development of the sporangium in all the living plants follows a common developmental pattern. In all cases archesporium is formed by the lower cell or cells cut off from the sporangial initial or a group of initials. The outer cells differentiate into the jacket initials. The archesporial cells by further division become sporogenous cells or spore mother cells, which undergo reduction division to form the spores. This is the common basic pattern of sporangial development.

Differences are, however, there in the details of development in different groups of plants. These are:

1. Whether the sporangium arsises from a single initial or a group of initials.

2. The number of cells making up the primary archesporial tissue.

3. Whether the archesporial cells act directly as spore mother cells or they divide mitotically and then act as sporocytes (spore mother cells).

4. Number of functional sporocytes.

5. Number of spores which mature.

6. Origin of the tapetal layer and its time of disorganisation.

A few of these differences have played a role in the development of heterospory. These comparative and developmental studies illustrate the various pathways that have led to heterospory. The time at which the sex determinants activate and exert their influence to segregate sex seems to play a major role in illustrating the different developmental pathways leading to heterospory. The following examples will illustrate the statement.

In the homosporous vascular cryptogams, *e.g.*, *Lycopodium*, *Dryopteris*, *Pteridium*, etc., the sex determinants exert their influence during the development of the sex organs. In *Equisetum* Hauke (1963) observed that the gametophytes that are all alike in early stages of development show distinction into two types during further vegetative growth and it is easy to determine which will bear antheridia and which archegonia. In this case the sex determinants exert their influence earlier, *i.e.*, before the formation of sex organs. In these cases sex determinants exert their influence in the gametophytes, their time, however, differs. In *Selaginella*, which is a heterosporous vascular cryptogam the sex determinants exert their influence during the differentiation of the sporocytes (spore mother cells). In the sporangia destined to develop into megasporangia only one megasporocyte is functional, whereas in the microsporangia all the sporocytes are functional. From this stage onwards there is clear differentiation between the two types of sporangia that will produce two types of spores that in turn develop into [illegible] same is the case in *Marsilea* and [illegible] ime of activation of sex determina[illegible] to the sporophyte. It is a small s[illegible] ought along with it the condition [illegible]

[illegible]

the maturation of the sporophylls. In many gymnosperms and some angiosperms the reproductive bodies are borne on special branches which can be identified before they bear the reproductive bodies. This can be ascertained [illegible] In these cases the sex determination occurs [illegible] branch. So in the seed plants the sex [illegible] much earlier than in the heterosporous [illegible]

These examples indicate that the phenomenal shift of sex determinants from gametophyte to sporophyte has accompanied heterospory.

Recently a case of incipient heterospory has been discovered in a fern called *Platyzoma microphylla* (Tryon, 1964). In this fern the sori contain two types of sporangia that are intermingled. In one type there are 16 large spores and in the other 32 small spores. The smaller ones germinate to produce male prothalli whereas the larger ones produce female prothalli But the female prothalli in case of failure of fertilisation may bear antheridia at a later stage. Incipient heterospory in also observable in *Ceratopteris thalictroides* (Schedlbauer, 1972). Multispore cultures of this species produce twotypes of prothalli. These are spathulate male prothalli and cordate bisexual prothalli. Such a distinctness in the genders is due possibly to the effect of an anthridiogen.

(c) **Experimental Evidences.** Only a few experimental studies have been conducted to approach the problem of origin of heterospory. All these studies were conducted with the basis that differences in spore size are due to abortion of most of the spores, greater abortion leaving greater nutrition for the remaining and functional spores, that grow in size. Shattuck (1910) performed a series of experiments on *Marsilea* and tested the effect of nutrition on spore size. He was able to alter the spore size by growing plants under variable conditions of light, temperature and nutrition. He found that in plants growing under favourable circumstanes the microsporangia contained a number of aborted microspores. The functional spores enlarged, grew larger in size, and it was found that spore enlargement was proportional to spore abortion. He found that the microsporangia showing microspore abortion developed spores that were 16 times larger than their original size. In extreme cases of abortion only a single spore survived and looked like a megaspore and showed all the structural characteristics of a megaspore. Under unfavourable conditions Shattuck (1910) was able to induce the formation of the large number of smaller spores in the megasporangia. He attributed these induced changes in the spore size to be due to change in the nutritional state of the sporangia. It was not possible for him to germinate these altered spores and therefore no conclusive results could be achieved. It was not possible to determine whether the larger spores (developed in microsporangia) germinated to give rise to the female gametophytes and smaller spores (developed in megasporangia) germinated to form male gametophytes. In the absence of such a conclusion these experimental studies cannot throw any light on the origin of heterospory.

Variations in the nutritional environments of the sporangia may alter the pattern of spore formation, but it appears that it is something else in the cellular control system that regulates the differentiation of spores into two different sexual entities. It depends upon factors in the genetic system of the cell.

HETEROSPORY AND SEED H

(a) Histolo..

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...nsidered in tracing the

Selaginella, no doubt, illustrates an example of heterosporous vascular cryptogams, that approach seed habit because of the following notable characteristics;

1 It is heterosporous

2. The megaspores start germination within the megasporangia and their time of release from the megasporangia varies with species

3 The number of megaspores in *S. rupestris* and *S. monospora* is reduced to one

4. In *S. rupestris* the megaspore is never shed and fertilisation and development of embryo up to the formation of rhizophore, stem and cotyledons takes place while the megaspore is enclosed within the megasporangium, which retains its connection with the parent plant. This condition can be linked to **Vivipary** in some angiosperms.

After ...

re ... can, however,
Se. ... ...yptogams like

... have no protective structure like the integuments surrounding their megasporangia.

2. The retention of megaspores permanently within the megasporangia has not become established

3. Histological union between the megaspore and the megasporangium is absent (Martens, (1966)

4. Lack of resting period after the development of embryo.

The ... ...comparable to the ...ained megaspore to ... The endosperm in ... *Selaginella*. Both ...ers. In *Selaginella* ...ll of *Selaginella* is ... and could easily act as a protective structure. As a matter of fact the outermost wall of megasporangium in *Selgainella* ... at maturity. It could easily ... embryo. There is no structure ... plants in the megasporangium

Regarding the retent...

union between the megaspore wall and the wall of the megasporangium. In the presence of such a union, the megaspore could never come out of the megasporangium. Such a union if present in *Selaginella*, could also usher in an era of rest for the embryo after its development. In such a case the whole megasporangium could have fallen down from the plant and a megasporangium with contained embryo could easily be regarded as a primitive seed. In case we find a living example of a seed plant in which there are traces of separation of megaspore from the megasporangium we can regard it as a clue of the origin of seed habit. Martens (1966) has worked on these lines and has arrived at a more or less safe conclusion. Weterkeyn and Sloover (1962) c[illegible] microspores of certain seed pla[illegible] and found that a deposition [illegible] g the spores [illegible]

[illegible] megasporocyte callose. [illegible]

separation betw[illegible] is evident. It is n[illegible] of gymnosperms. [illegible] gametophytes ... porocytes has been made. It can be presumed that such an isolation mechanism of [illegible] might have been present in the [illegible]

"However if i[illegible] authentically r[illegible] that it was al[illegible] version in Fre[illegible] the living ... [illegible]

observations c[illegible] between the Cycadophyta and Coniferophyta."

CHAPTER VII

SPHENOPHYTA (Benson, 1957)

The [illegible] lso known by two other names. One of hese Arthrop ıyta [illegible] the oldest name. Smith (1935) suggested the name Calamophyta [illegible] : (*i*) The sporophytes are [illegible] n some the stem is jointed, [illegible] have solid or medullated [illegible] some extinct members ; [illegible] ty are homosporous, some [illegible] ia arise in whorls on the [illegible] he vegetative leaves ; (*iv*) [illegible]

A. Class :—Sphenophyllopsida. It includes only one order. They are all extinct.

Order Sphenophyllales. The representatives of the order are distributed among two extinct families. They appeared on this earth in the Upper Devonian and persisted till the lower Triassic.

Family 1. Sphenophyllaceae. It includes the genera *Sphenophyllum, Sphenophyllostachys, Bowmanites and Eviostachya*. All of them are extinct.

Family 2. Cheirostrobaceae. It is represented by the genus *Cheirostrobus* that was discovered in the Lower Carboniferous of Scotland. It was a large cone measuring 3·5 cm. in diameter.

B. Class ;—Calamposida. It includes three orders :

Order 1. Calamitales. This order was at its peak of development during the Upper Carboniferous along with the Lepidodendrales and were found in the coal measures and swamp forests. The order became extinct at the end of Permian. It includes two families.

Family 1. Asterocalamitaceae. It includes the genera *Asterocalamites* and *Archaeocalamites*. They are extinct.

Family 2, Calamitaceae. It includes the genera *Calamites, Protocalamites, Annularia, Asterophyllites, Protocalamostachys*, and *Palaeostachya*.

Order 2. Hyeniales. They are represented both in the Lower and Middle Devonian and include two families.

Family 1. Protohyeniaceae. It includes the genus *Protohyenia* that was discovered by Ananıev (1957) from the Lower Devonian rocks of Siberia.

Family 2. Hyeniaceae. It includes the genera *Hyenia* and *Calamophyton*.

Order 3. Equisetales. It includes the family Equisetaceae that is represented by one extinct and one living genus. *Equisetites* is the extinct genus and *Equisetum* is the only living genus of the division Sphenophyta.

EQUISETACEAE

The family includes a single living genus *Equisetum*, which is represented by twenty-five species. It is the only living represen-

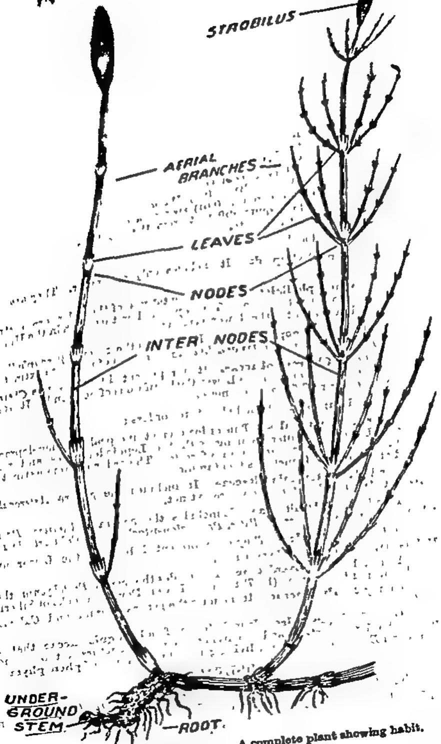
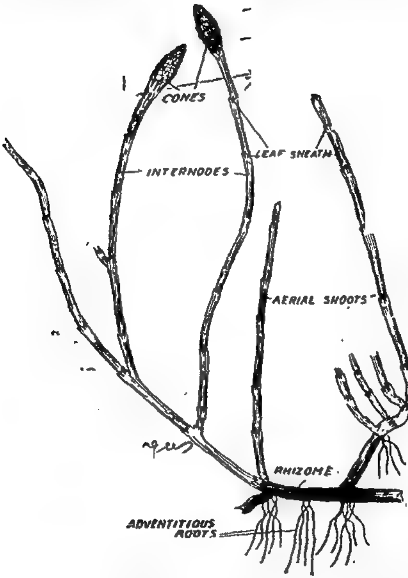


Fig. 7·1. *Equisetum diffusum.* A complete plant showing habit.

...ative of the entire race, that has become extinct. The family has certain characteristic features of its own, that are listed below :—

1. The stems are jointed and have distinct nodes and internodes. The underground part of the stem is the rhizome and bears numerous aerial branches.



...2. *Equisetum debile.* A complete plant showing habit.

...e internodes are longitudinally ribbed so that there are distinct ridges and furrows. The ridges and furrows of each internode are not continuous but alternate with each other.

3. The leaves are small and scale like and are arranged in whorls on the nodes. The members of a whorl on a node are united to form a sheath around the node. The free edges of the leaf sheath are opposite the grooves.

4. The aerial stem may be branched or unbranched. When th e branches arise in whorls at the nodes and always alternate

leaves. The branch primordium pierces through the base of the leaf sheath and then grows into a branch.

5. The stem is green in colour and performs the photosynthetic functions. It has developed sclerenchyma below the ridges. The chlorenchyma is also well developed. The stomata are restricted to the grooves.

6. The anatomy of the stem reveals that it possesses both hydrophytic and xerophytic characteristics. Presence of vallecular cannals and carinal canals and feebly developed xylem are the hydrophytic characteristics. Presence of a rough cuticle, ridges and grooves and sclerenchyma are the xerophytic features. Reduced leaves are also a xerophytic character.

7. The stelar arrangement is essentially an endarch siphonostele, which in the internodes has separate collateral vascular bundles.

8. The strobili are compact and have peltate sporangiophores that are arranged in whorls. The sporangia arise from the lower or inner surface of the peltate disc and are elongated sac like structures. They terminate the main axis or the branches.

9. They are homosporous.

10. The gametophytes (prothalli) bear both male and female sex organs but unisexual prothalli are not rare.

11. The prothalli are exosporic in *Equisetum*.

12. The spermatozoids are multiciliate.

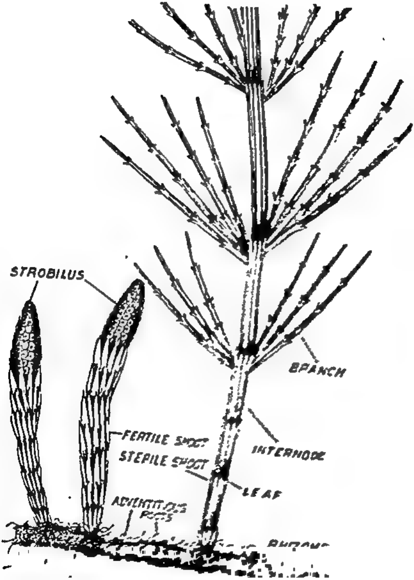
EQUISETUM

Distribution. The twenty-five species of *Equisetum* are widely distributed and reach luxuriant development in the North Temperate zone (N. America, Eurasia). Some occur in tropical regions (W. Indies, S. America, Chile) ; rare in arctic and alpine zones. [illegible] into S. Africa. It [illegible] India (Narkanda near [illegible] l Australia. In India [illegible] -um, *E. arvense* and [illegible] n Malaya and some Pacific islands. A fossil form was known in Cretaceous times.

Habitat. *Equisetum* grows under varied habitats, but thrives [illegible] -ile grows under [illegible] conditions This [illegible] survive the test [illegible] they are found [illegible] *pratense*) and swampy places (*E. palustris*). *E-arvense* grows in open grass lands, railway embankments, exposed sandy and dry places and at various altitudes on the hills.

[illegible] -ipdermal cell walls of [illegible] -rted the presence of [illegible] -ice of silica gives a [illegible] to this bundles of [illegible] earned the genus a [illegible] are of great medi- [illegible] diuretic in Germany. The ashes of this plant are used to relieve acidity and dyspepsia.

E. debile yields a cooling medicine that relieves gonorrhoea. The stems of *E. hyemale* are used for polishing.



Habit. The
in size. They are
perennial, and muc
number of aerial b
the aerial branches pres
of distinct nodes and
during unfavourable per
in some species they
species (*E. scripoides*) has a few inches high aerial shoots with 1 to 1½ mm. across; the largest (*E. giganteum*) has 6-13 meters tall aerial stems with 2·5 cm. across and are unable to stand erect. *E. schaffneri is stout with 2·5 metres high stem and 10 cm. in diameter.* The common Indian species *E. debile* is 1—2 feet high under xeric conditions but grows up to 2—5 metres tall under damp and shaded environs. In tall species the stem is weak (½ to ¾ cm. across). *E. arvense* is medium sized.

Stem. The main stem is an extensively branched sympodial, dark brown or brown, rhizome that gives off branches from its nodes

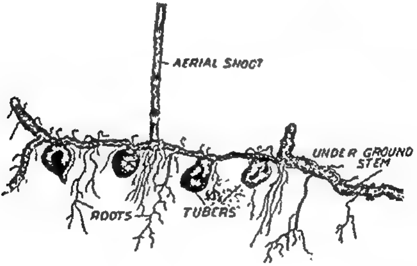


Fig. 7·4. *Equisetum arvense.* Rhizome with tubers.

(Figs. 7·1, 7·2, into the soil and gives off aerial s alternate with the brown scal heir bases and along a portion The branch primordia pierc d grow out as branches that may remain underground or become aerial, or may remain inactive for some period. In some species, *e.g.*, *E. arvense* (Fig. 7·3) the branch primordia develop into tubers whose cells store food material and are capable of perennating. These tubers are, therefore, branches whose growth becomes arrested. They represent a single internode.

Aerial Branches. They are always conspicuously jointed and are green rough ... ilica) and stiff,

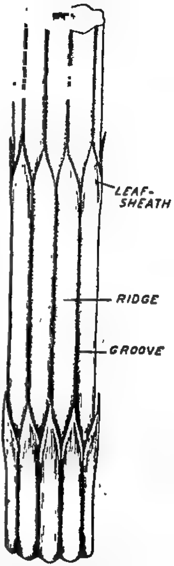


Fig. 7·5. *Equisetum debile.* Portion of an aerial stem showing ridges and grooves and their position in the respective internodes.

7·5) ... r of ... aves ... of ridges at successive nodes is usually disturbed due to the variation in the number of leaves in the upper nodes of the stem (Bierhorst, 1959). Another characteristic feature of the stem is the presence of an **intercalary meristem** that is present at the base of the internodes and just above the node. This meristematic region is protected by the leaf sheath. The activity of this meristem is responsible for the increase in length of the internode. Its presence makes the stem structurally weak. If we pull the stem, the internodes easily separate or are pulled apart at these weak spots. Due to hollow internodes the pulled apart pieces are often called the 'pipes'.

The aerial stems may be branched or unbranched. In *E. arvense* the sterile aerial branches are profusely branched (Fig. 7·3). The branches arise in whorls at the nodes. They alternate with the leaves. The branch primordia pierce through the leaf sheath at its base and then grow into branches. The number of branch primordia usually correspond to the number of leaves at a node. In *E. sylvaticum* the whorled branches on the main aerial stem may branch in turn. In *E. diffusum* (Fig. 7·1) the whorled branches do not branch in turn. In *E. hyemale* and *E. debile* the buds remain dormant throughout the life of the plant and the aerial stems are persistently unbranched. The dormant buds may resume activity if the apical bud is injured and whorled branches may develop.

In *E. debile* (Fig. 7·2) and *E. diffusum* (Fig. 7·1) the aerial branches show no distinction into fertile and sterile shoots. All of them are green and may bear terminal strobili.

or segments divides by an anticlinal wall into **segment cells** that are superimposed (*i.e.*, one lies above and the other below). This division of the segments into segment cells differentiates two tiers, the upper segment cells develop into nodes (by further division) and the lower by a periclinal wall into two unequal cells. The outer larger cell divides further and gives rise [illegible] The inner smaller cell divides [illegible] ssues are distinguished in the [illegible] he central pith cells disintegrate [illegible] nd Wetmore, 1948) and forms a hollow cavity. This appears during the elongation of the internode. Some of the cortical cells also are unable to keep pace with the elongating internode and result in their separation from each other. This is how the air cavities appear in the cortex. These air cavities are called the **vallecular canals.**

Good and Taylor (1972) have compared the shoot apices of *Equisetum* with the fossil genera *Sphenophyllum* and *Calamites* and have found them to be similar in many respects. They have remarked, "The similarities in the shoot apical organisations of *Sphenophyllum, Calamites* and *Equisetum*... show that this primitive type of apical meristem has undergone very little evolutionary change within the *Arthrophytina* since Pennsylvanian times (late Paleozoic)."

[illegible]

Root. The pyramidal and four-sided or teterahedral apical cell of the root has four cutting faces (in contrast to three in stem). The cells cut off by the fourth outer surface give rise to the root cap, whereas the cells cut off by the lower three faces give rise, as in stem, to the procambial strands, cortex and epidermis.

Anatomy

Stem (Figs. 7·6 to 7·9). In a cross-section the general outline of the stem is not circular due to the presence of ridges and grooves. The anatomy of the stem will be considered separately for internode, node of aerial stem, and the rhizome.

Internode of the Stem. If we examine the cross-section of a stem passing through the internode of an aerial branch, we will find the following layers of tissues in sequence :

Epidermis. This is a single layered tissue of the stem forming the strong outer covering. Their walls are cuticularised and covered with rods or grains of silica The silica strengthens the cell walls, prevents water loss through epidermis, protects against pathogens and predators, and helps in keeping the plants erect. Kaufman and his co-workers (1972) have shown that in *E. scripoides* the silica (SiO_2) deposits first in the stomatal apparatuses and later in the long epidermal cell walls, progressing through the top of the internode to the basal intercalary meristematic region in a basipetalous sequence They are of the opinion that silicifications must play a major role in *Equisetum* shoot development in breaking internodal extension, strenghening the shoot system and triggering "senescence" in last stages of internodal development". Here and there the epidermis is perforated by the stomata which are present in the

In *E. arvense* (Fig. 7·3) and *E* telmateia there is segregation of aerial branches into separate f
fertile shoots are nongreen, unbra
They die after spore dispersal. The
fusely branched, green and do not bear strobili (Fig. 7).

In *E. pratense* the unbranched, colourless reproductive shoots turn green and develop branches, after throwing off their mature strobili.

In *E. palustre* the rhizome bears three types of aerial branches on the same plant. These are the sterile, green and branched shoots; the fertile unbranched and colourless shoots that die after spore dispersal and fertile branches which behave like sterile branches after shedding their strobili.

A few examples of abnormal development of the shoot have been observed. These are: (*i*) internodes very small giving a stunted appearance; (*ii*) internodes flexuous and give a snake like appearance to the plant; (*iii*) dichotomous branching of the axis; and (*iv*) growth of vegetative shoot beyond the terminal cone.

Leaves. ... are simple,
e ... they arise in
v ... or even in
the same species. In species with narrow stems the number is less (2 to 3 in *E. scirpoides*) and in those species bearing thick stems, *e.g.*, *E. schaffneri*, the number is large (up to 40). Sometimes the stems go on becoming thinner towards the apex and in such cases the number of leaves at the lower nodes is more as compared to the upper nodes (Bierhorst, 1959). All the leaves at a node are laterally fused to form a sheath around the base of the internodes. The sheath has free and pointed teeth like tips. It is brown in colour and is closely applied to the internode. This is mainly protective in function and in some species the leaves become dead and scale like at maturity. The leaves do n
function, which is, therefore, confi
The members of a leaf whorl at
the upper or lower nodes.

Roots. The roots are generally borne on the rhizome and except the first root of the embryo, the rest are all adventitious and arise endogenously. They arise from the bases of the branch primordia at each node and are therefore borne in whorls. The roots are extensively branched and have a root cap at their tips.

Apical growth

Stem. It is effected by means of a single pyramid like and four-sided tetrahedral apical cell. The rounded base of the pyramid like apical cell is towards the outer free end of the stem. The apical cell cuts off segments along its three lateral sides only. These are called cutting faces and are directed downwards. The apical cell cuts off three (one on each cutting face) cells and this process continues in a successive manner. Each of these cells

or segments divides by an anticlinal wall into **segment cells** that are superimposed (*i.e.*, one lies above and the other below). This division of the segments into segment cells differentiates two tiers, the upper segment cells develop into nodes (by further division) and the lower by a periclinal wall into two unequal cells. The outer larger cell divides further and gives rise to the procambial cells, **cortex and epidermis**. The inner smaller cell divides to form the pith. Like this the primary tissues are distinguished in the node and the internode. In the internode the central pith cells disintegrate by a process of mechanical tearing (Golub and Wetmore, 1948) and forms a hollow cavity. This appears during the elongation of the internode. Some of the cortical cells also are unable to keep pace with the elongating internode and result in their separation from each other. This is how the air cavities appear in the cortex. These air cavities are called the **vallecular canals.**

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Leaves. The first primordium of a whorl of leaves first becomes visible as a ring at the base of the apical cone of the stem. This ring of initials grows to form the basal and fused portion of the leaf sheath. Another set of initials appears around the upper margin of the sheath and grows to form the free tips of the leaves.

Root [illegible]

Anatomy

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nodal e[illegible]
cence" [illegible]
epiderm[illegible]

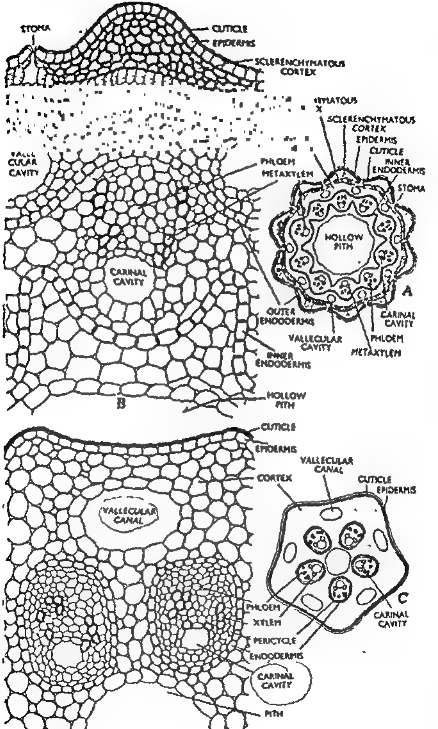


Fig. 7·6 (A—D).

Equisetum debile Anatomy of aerial stem and the rhizome. A. T S. diagrammatic passing through the aerial internode of the stem. B. T S. Portion in detail. C. T.S. diagrammatic passing through the rhizome. D. T.S. Portion in detail.

furrows. The stomata (Fig. 7·7, A, B) are peculiar in having a double set of cells, lying one above the other. The two innermost cells constituting a pair of **guard cells** and the two uppermost a pair of **accessory** or **subsidiary cells** (Fig 7·7). The subsidiary cells completely cover the guard cells and hide them from view. A number of transverse bands of siliceous matter radiate from the stomatal pore and traverse the guard cells (Fig 7·7, B). The stomata in some species are sunken, each lying in a pit. In some species the stomata are on the surface. The stomatum develops from a single superficial cell called the stomatal initial. It divides by two longitudinal walls into three cells. The middle cell acts as the **guard mother cell** whereas the two lateral cells act as **subsidiary cells.** The guard mother cell divides again by a longitudinal wall to from two guard cells. A pore appears between the guard cells. Later the subsidiary cells grow over the guard cells and overarch them. Such a developemental pattern of the stomata recalls the syndetocheilic type of stomatal ontogeny found in some fossil groups of the gymnosperms (Bennettiales). Such an affinity has been pointed out by Pant and Mehra (1964) while discussing the development of stoma in the vascular cryptogams.

The siliceous bands of thickening have been regarded by some authors (Campbell 1911 ; Johnson 1933 ; Copeland 1936 ; Kersimo 1954) as belonging to the guard cells. Others (Hauke, 1957 ; Jyotsana, 1964) consider them to arise from the inner walls of the subsidiary cells.

Cortex. The many layered cortex is differentiated into a variety of tissues (Fig. 7·6). It can be conveniently divided into two parts (*i*) outer cortex and (*ii*) inner cortex. The outer cortex is differentiated into two types of cells :—

(*i*) **Sclerenchymatous Cells** (Fig. 7·6). These are thick walled cells that give mechanical strength to the stem and are sub-epidermal in position. Below the ridges, they occur in large and heavy groups. There is an equal number of smaller groups of sclerenchyma beneath the epidermis of the grooves or the furrows. They are absent beneath the stomata. They are very well developed in *E. giganteum* and project to sufficiént depth in cortex. The cells are dead and colourless and mainly perform mechanical functions. They have been designated as fibre like collenchyma by Hauke (1963).

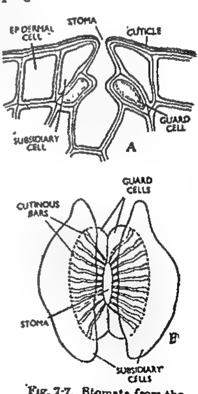


Fig. 7·7. Stomata from the stem internode of *Equisetum*.
A. T.S. epidermis of *E. arvense* showing sunken stomata. B. stoma of *E. telmatia* showing siliceous bars.

(ii) **Chlorenchymatous cells.** These are lying lateral to and below the sclerenchyma (forming a curved band) and contain a large number of chloroplasts in their cells and form the assimilatory region of the stem (Fig. 7·6). From below the sclerenchyma of the ridge it reaches the surface on either side between the support tissue of the ridge and that of the furrow. Here lie the stomata, therefore, communicating directly with the green tissue. *E. debile* (Fig. 7·6) reveals a continuous band of chlorenchyma composed of elongated cells arranged in 3 or 4 layers below the sclerenchyma.

Inner Cortex. It consists of a few layers of larger celled parenchyma traversed by a ring of large air spaces (Fig. 7·6) forming an aeriating system. They are called the **vallecular canals.** Each of these lies below the furrow of the external surface and is thus close beneath the photosynthetic tissue.

Presence of sclerenc [illegible] and sunken stomata are the xe [illegible] ridges [illegible] Presence of [illegible]

Endodermis. A variety of conditions is found as to the position of endodermis in various species. The most common condition as is found in *E. arvense*, *E. palustre*, *E. scripoides* and a few other species is that a common ring of endodermis is present surrounding the whole ring of the vascular bundles on their outside (Fig 7·8). In other species a common ring of endodermis is present both outside as well as inside the vascular bundles as in *E. debile* and *E. hymale* (Fig. 7·6). The outer endodermis dips in between the vascular bundles, in some cases, coming to lie against the inner endodermis. In *E. limosum*, *E. giganteum* and a few other species there is a separate endodermal layer encircling each vascular bundle. Some botanists consider the first condition to be the most primitive and the last the most specialised. Evidences for this are derived from comparative studies of stelar structures in the genus and from the structure of the *Calamites*, an ancient group related to *Equisetum*.

Stele. Within the endodermis there is a single layer of pericycle forming the outermost layer of the stele. The stele consists of a well defined [illegible] vascular bundles surrounding a large pith cavity. The [illegible] They alternate in [illegible] beneath the ridges. [illegible] one another by a large zone of parenchyma [illegible] bundles and so beneath the ridges are smaller carinal cavities. One of these belongs to each vascular bundle and is filled with water. The carinal canals are formed by the tearing apart of the protoxylem elements. Since protoxylem distinguishes itself quite early during [illegible] the elongating internodes exert a tearing effect [illegible] of water

vascular bundle consists of xylem and phloem. There is no cambium hence the bundles are closed.

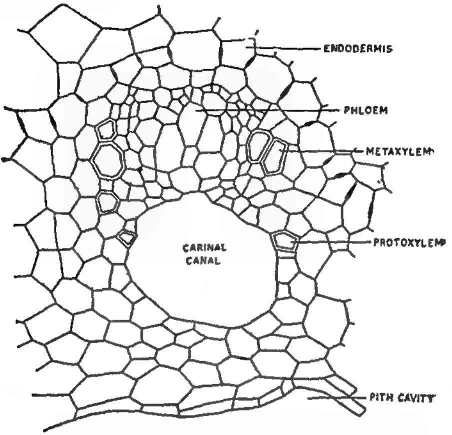


Fig. 7 8. A vascular bundle from the aerial stem of *E. arvense*. The endodermis is present only on the outer side of the bundle.

Xylem is poorly developed. It has the shape of a "V". The point of "V" lies towards the centre and the ends diverge towards the outside. The metaxylem which consists of scalariform tracheids form the two limbs of the "V". Bierhorst (1958) studied in detail the xylem elements in some species of *Equisetum* and reported the presence of two types of vessel elements in the metaxylem of internodes alone One type of vessels have simple perforation plates and the other type have reticulate. He reported that the vessels occur only three in a row and do not form long conducting channels as in seed plants. The protoxylem which occupies the point of "V" consists of a few annular and spiral tracheids. Later on, its position is occupied by the carinal canals as a result of its disorganisation. The meta and protoxylem are separated from each other by a little parenchyma.

Bierhorst (1958) has, however, reached a different conclusion as a result of his studies on the xylem of 10 species of *Equisetum*. He observed that the metaxylem groups occupying the lateral arms of

"V" are quite independent of the few xylem elements and carinal cavity. He regards it as carinal groups of xylem because according to him carinal canal is a conducting channel. He found that the carinal group has its own metaxylem and protoxylem so do the xy- [illegible] 'V'. The *lateral* xylem group may [illegible] up of protoxylem (*E. fluviatile*), or of [illegible] etc.) *or of both proto* and metaxylem (*E. sylvaticum*).

The phloem consists of phloem parenchyma and the sieve tubes. It lies between the two *limbs* of the "V" but a little to the outer side (7·9).

Pith. The pith is present in young specimens but *is* absent in the mature stems and *is* represented by a large central cavity (Fig. 7·6).

Node. The anatomy of the node shows some difference from that of the internode. Vallecular canals are present in some species (*E. debile*), and *may* be absent in others. The pith is present at the [illegible] internodes above and [illegible] absent in the nodal [illegible] presence of protoxylem groups in place of carinal canals. Eames (1909) and Bierhorst (1958) are of the view that the protoxylem elements are present. Some, however, regard it to be absent The continuous vascular cylinder of the modes *give rise to the* leaf traces and the branch traces. Some workers regard the separate vascular strands of the internodes *as leaf* traces that extend down the internodes of the node below. This view is, however, not held to be correct. Another view regarded the stelar system to be a **dictyostele** and the prenchymatous gaps between the bundles as leaf gaps. This is also untrue as the leaf traces in microphyllous pteridophytes do not leave any leaf gaps. *Moreover this* view is not supported by the studies on the extinct relatives of *Equisetum*. *This view also* overlooks the presence of intercalary meristem whose activity is responsible for growth in length of the *internode*. The nodal vascular *cylinder* must be looked upon as a siphonostele. The appearance of the parenchymatous gaps in the internode *may* be due to some activity of the intercalary meristem.

Rhizome (Fig. 7·6, C, D and 7·9). It differs from the aerial stems in certain respects ; (*i*) There are no stomata in the epidermis ; (*ii*) the sclerenchyma is not very well developed and forms a conti- [illegible] (*iv*) the pith is present in [illegible] In *E. debile* the endodermis [illegible] in *E. arvense* a common endodermal layer encircles the stelar region externally (Fig. 7·9).

The fertile aerial shoots of *E. arvense* are colourless and a transverse section reveals the absence of stomata in the epidermis. The

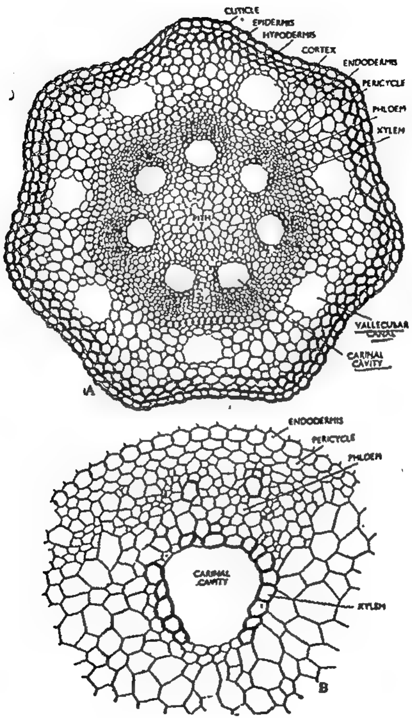


Fig. 7·9 (A-B). *Equisetum arvense.* A. T. S. portion of rhizome showing detailed internal structure. B. A portion of above showing a structure of a bundle in detail.

sclerenchyma and chlorenchyma are also absent. The rest of the structure is similar to that of the rhizome. In *E. sylvaticum* the colourless fertile shoots become green and act as ordinary sterile shoots after the dispersal of spores. In this case the stomata, the sclerenchymatous tissue and the chlorenchyma appear after the spores are shed.

Strobilus. The anatomy of the strobilus is similar to that of the nodal region. In this region the vallecular canals and the carinal canals are absent. The protoxylem is well developed and forms a continuous internal or endogenous band. It is separated from the external metaxylem by a few layers of parenchymatous cells. The metaxylem is very well developed in the mature cones and forms a continuous strand made up of two to four layers of metaxylem tracheids. The vascular cylinder of the strobilus gives off traces to the sporangiophores which do not leave any gap in the stele. These traces traverse the sporangiophore stalks and on entering the peltate disc undergo repeated forking or branching. Each branch terminates at the base of the sporangium.

Nature of the stele and gaps. Recent studies on the developmental anatomy of the axis of *Equisetum* (Golub and Wetmore, 1948) reveal a complete absence of the foliar and branch gaps in the stelar organization. The parenchymatous areas between the vascular bundles in the internode have been regarded by these authors to be ground tissue parenchyma. It might have developed due to the activity of the intercalary meristem. The observations suggest that the stelar organization in the stem of *Equisetum* is purely a siphonostele which forms a complete and uninterrupted cylinder at the nodes. At the internodes its continuity is interrupted by the appearance of parenchymatous areas that are neither foliar gaps nor branch gaps.

Earlier workers like Browne (1912, 1915, 1920, 1921, 1933) suggest the presence of leaf gaps in region of the strobilus and she regards the sporangiophores as modified leaves. Moore (1941) also agrees with Browne. Jeffery (1917) regards the parenchymatous areas between the vascular bundles in the internode as branch gaps. Barratt (1920) conducted a detailed study on the development of the vascular tissues in *E. arvense* and *E. maximum* and regarded these gaps to be due to the encroachment of parenchyma on the xylem tracheids. Studies by Barratt reveal that the stele in the first embryonic shoot is a typical protostele. It changes to a siphonostele at the point where a secondary branch originates. All branches that arise later have an [illegible]terrupted siphonostele at their bases. The same is the case at the nodes. [illegible] the internodal regions alone the continuity is interrupted by the appearance of parenchymatous gaps, which according to Barratt are due to encroach[illegible] the ground tissue parenchyma. These studies were later confirmed [illegible] (1944) as his studies on *E. limosum*. These detailed onto[illegible] therefore, support the view that there are no leaf gaps in stelar set-up of *Equisetum* and the stelar organisation is

(Sykes, 1903; Sahni, 1925). These observations have suggested a new concept of evolution of stele (see Chapter 8).

Root (Fig. 7·10). The outermost layer of the root is the single layered epidermis or the piliferous layer. It bears root hair in the root hair zone. It is made up of a single layer of thin walled cells.

Underneath it is the many layered cortex consisting of parenchymatous cells. The larger roots in *E. limosum* and *E. debile* possess a row of large air spaces in the inner cortex (Fig. 7·10). These spaces develop schizogenously. In some species the cortical cells beneath the epidermis are thick walled and lignified. They constitute the tissue usually referred to as **exodermis.** Cortex is limited on the inside by a well defined endodermis followed by a pericycle which is one cell thick. Since the cells of the pericycle fit accurately

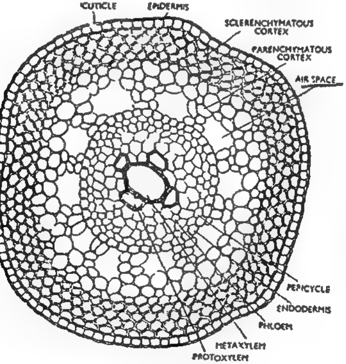


Fig. 7·10. T.S. root of *E. debile.*

to those of the endodermis, some botanists like Smith consider the endodermis to be two cells in thickness. Since there are no casparian strips in the pericycle cells, it cannot, therefore, be regarded as a second layer of endodermis. Casparian strips are, however, clearly visible in the outer layer. Lateral roots originate from the pericycle. The stele is triarch or tetrarch. The three or four protoxylem groups meet and surround a central metaxylem vessel. There is no pith. The phloem elements alternate with the protoxylem groups. Both the xylem and the phloem are exarch because both the protoxylem and the proto-phloem lie towards the periphery.

The above account shows that the *Equisetum* sporophyte is remarkable for mingling of hydrophytic and xerophytic characters in its structure.

VEGETATIVE PROPAGATION

In some species the primordia on the rhizome remain short [illegible] tubers [illegible] tached [illegible] d thus [illegible] The [illegible] a outer thick walled protective layer of cells.

Every branch of the rhizome bears preformed branch primordia which can develop into new subterranean and aerial branches [illegible] the deep seated rhizome may [illegible] branch with the help of pre- [illegible] become active (from the hor- [illegible] plant. The aerial shoots can [illegible] ch node-internode segment of the aerial stem has the potentiality of giving rise to a new plant. Such preformed primordia are also present in the normally unbranched species. The root primordia are always associated with branch primordia at their bases and hence there is no difficulty in establishing the new vegetatively developing plants.

REPRODUCTION BY SPORES

The spores of *Equisetum* are of one [illegible] developed [illegible] different [illegible] together [illegible]

ORGANISATION OF THE STROBILUS

Position. [illegible] nation and liberation [illegible] rminal and solitary. [illegible] *fusum*, etc.) there is no [illegible] s and every main aerial shoot bears a terminal strobilus (*Fig.* 7·1). In such cases the aerial shoots perform the dual function of photosynthesis and reproduction (*E debile*). In *E. arvense* and some other species there is segregation between fertile and sterile aerial shoots. The former are short, unbranched, yellowish and bear a terminal strobilus, whereas the latter are robust, green and profusely branched (Fig. 7·3). In *E. debile* the strobili mature in September and October. The whorled branches of aerial shoots do not bear strobili, except under exceptional conditions. The strobilus may be **apiculate** when the strobilus axis grows a little beyond the upper whorl of sporangiophores and becomes pointed. In others the strobilus has a rounded apex and bears sporangiophores at its apex.

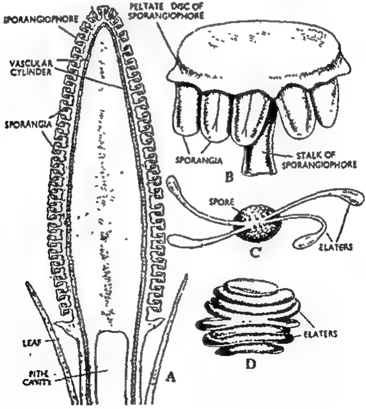
Abnormalities

A few abnormalities have been recorded in *E. debile* regarding the strobilus. In some cases it has been noticed that in addition to the terminal cone borne on the main axis there are present lateral branches arising from [illegible] some cases two [illegible]

threaded upon an axis; or of a succession of such zones separated by leaf sheaths. It is thus seen that the strobilus of *Equisetum* is not always that circumscribed terminal body which is typical for the living species.

Structure of Strobilus

The cone of *Equisetum* is peculiar. It consists (Fig. 7·11, A) of a central thick axis which bears a number of densely crowded



re. ... to stems than to the
as ...
leaves.

Structure of Sporangiophore

... axis of the ...
sporangiophores. The peltate heads of the sporangiophores fit ... mutual ... At ... h the
annulus. ... s the
annulus is toothed and apparently represents reduced leaf whorl. It seems to some extent a protective structure. Some botanists consider it to be sporangiophoric in nature because the annuli of some species regularly bear small sporangia (*E. cryptophora*).

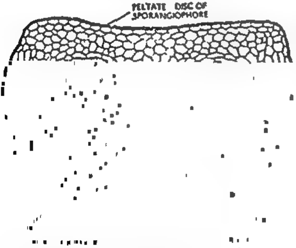


Fig. 7·12. L. S. of sporangiophore of *E. debile* showing two mature sporangia containing spores.

Sporangia. A mature sporangium is an elongated sac like structure (Fig. 7·12) full of large number of haploid spores. The spores are of equal size (homosporous). The mature sporangium has a *single layer* of wall cells. The cell walls of this layer are spirally thickened. A young sporangium has 2—4 layered thick wall. The innermost wall layer is derived from the outermost sporogenous cells and is called the **tapetum**. The *inner* wall layers and the tapetum disorganise as the spores are formed.

Dehiscence. [illegible] and [illegible] separ[illegible] [illegible] unity and are carried away singly or in clusters by the air currents.

Spores (Figs. 7·11, C—D and 7·13, A—E). The spores when young are green and are covered by a thin wall of cellulose. At maturity they are relatively larger, rounded and contain numerous chloroplasts (Fig. 7·13, A—C) and have a thick spore wall differentiated into four layers (Beer, 1909). These layers are the outermost **epispore**, middle **perispore**, third layer called the **exospore** and

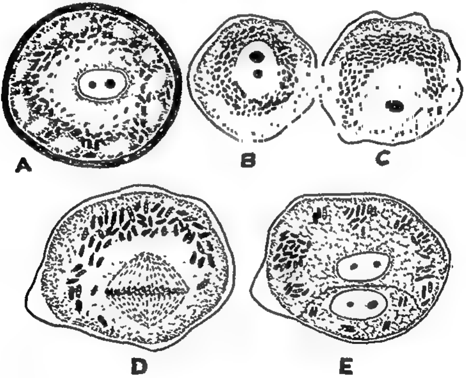


Fig. 7·13. (A—E). *Equisetum. Early stages in spore germination.*
A. Mature spore of *E. arvense* containing large plastids (After Py).
B. Chloroplasts radially arranged around the nucleus (After Nienburg).
C. [illegible]
D. [illegible]
E. [illegible]

the innermost **endospore** or **endosprium**. The epispore becomes divided along several spiral lines into two long bands which until maturity remain closely wound around it. Bierhorst (1971) states that the elaters are deposited on the outer spore wall by the "free

of the sporangiophores (Fig. 7·14). Further growth results in the formation of a constriction near the base of these outgrowths thus differentiating a lower stalk and the upper peltate disc. The stalk increases in length and carries the disc away from the axis.

side of the peltate disc near the

ever, all the sporogenous tissues in a sporangium can be traced back to a single superficial cell of the young sporangiophore.

primary sporogenous cell

to give rise to a mass of sporogenous cells. The outer cell

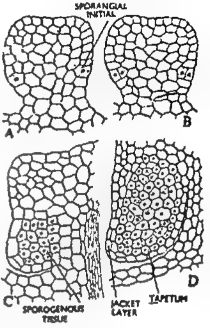


Fig. 7·14. Stages in the development of a sporangium in *Equisetum arvense*.
A. a young sporangiophore in L.S. showing two sporangial initials.
B. L.S. sporangiophore with sporangial initial divided into an outer and inner cells.
C. A later stage of development.
D. L.S. sporangiophore with young sporangium.

sporangium. The inner layers
ng with the sporogenous tissue
The cells of the sporangi-
the outer
the sporangial wall It therefore
wall is not
cells divide
wall layers
of the last cells. About 1/3 of them degenerate along with the tapetal cells. The surviving or functional spore mother cells round off and float in the **periplasmodial fluid** formed by the degenerated tapetal cells and the spore mother cells. The inner wall layers, except the outermost layer, also degenerate The rounded spore mother cells undergo meiosis and form tetrads of haploid spores. Later the spores secrete their own

liquid" in the ... The bands are detached from each other ... f the bands are slightly expanded ... They are known as **elaters** and are ... s (Fig. 7·11, C). They are hygro- ... the spores in moist air. When dry the elaters ... remaining attached only ... int so that they appear as ... those of the bryophytes as they ... cells. The elaters in bryophytes ... spiral thickenings, whereas in *Equ* ... no spiral thickenings. The spores ...

Functions of Elaters

The elaters help in the dispersal of spores and dehiscence of the sporangium. At maturity the sporangiophores wither and the sporangia lose water ... *elaters.* T ... more room ... gives in an ... that as th ... prothalli.

Incipient Heterospory

The spores of *E. arvense* are apparently all alike and the species is said, therefore, to be homosporous. McClean and Cook (1951) reported the occurrence of two kinds of spores in *E. arvense.* They examined a large number of spores and measured their diameter and plotted them on square paper. It was found that two curves are produced with separate maxima and very little over-lapping. The smaller series are much pale green than the larger ones and can be picked out by eye in a fresh sporangium. The two kinds are not equal in number nor is the number in ... (Schratz, 1928). This is a kind of incipient heterothallism. The case is interesting, however, as showing apparently an early stage in the development of heterospory.

Development of Sporangia

The aerial shoot destined to give rise to the strobilus at its tip exhibits very slow apical growth and assumes a conical shape. It soon shows small conical protuberances that arise in an acropetalous succession (younger near the apex and the older below). These outgrowths assume a hemispherical shape and are the primordia

of the sporangiophores (Fig. 7·14). Further growth results in the formation of a constriction near the base of these outgrowths thus differentiating a lower stalk and the upper peltate disc. The stalk increases in length and carries the disc away from the axis.

[illegible]

ever, all the sporogenous tissues in a sporangium can be traced back to a single superficial cell of the young sporangiophore.

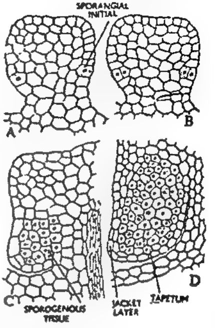


Fig. 7·14. Stages in the development of a sporangium in *Equisetum arvense*.

A. a young sporangiophore in L.S. showing two sporangial initials.

B. L.S. sporangiophore with sporangial initial divided into an outer and inner cells.

C. A later stage of development.

D. L.S. sporangiophore with [illegible]

The sporangial initial divides into an outer and an inner cell by a periclinal wall. The inner or the primary sporogenous cell [illegible] divides periclinally as well [illegible] layers [illegible] tissue [illegible] the sporangial wall. It therefore [illegible] wall is not d[illegible] cells divide [illegible] functional spore mother cells round off and float in the periplasmodial fluid formed by the degenerated tapetal cells and the spore mother cells. The inner wall layers, except the outermost layer, also degenerate The rounded spore mother cells undergo meiosis and form tetrads of haploid spores Later the spores secrete their own

wall layers and separate as individual spores. The spores contain chloroplasts and are surrounded by 4 layered wall. The sporangial wall cells becomes spirally thickened.

MORPHOLOGICAL NATURE OF THE STROBILUS AND THE SPORANGIOPHORES

The strobilus of *Equisetum* has been regarded by some authors (Browne, 1912, 1915, 1920, 1921, 1923, 1927, 1933) to be a shortened axis differentiated into nodes and internodes. The sporangiophores have been regarded to arise from the nodes. Barratt (1920) on the other hand regards it to be a shortened axis without any differentiation into nodes and internodes. The former view is supported by many botanists.

The morphology of sporangiophores is a debatable question and a number of explanations have been forwarded. Milde (1867) regarded the sporangiophores to be modified leaves. From his extensive and excellent observations on the transitional forms between the sheath leaves and the annulus teeth, and between these teeth and the sporophylls, Milde arrived at the firm conviction that leaf, annulus teeth, and sporangiophores [illegible] Goebel also came to the same conclusion. [illegible] this view. He was able to [illegible] shoots. The sporangiophores exhibited a regular change to ordinary leaves during his experiments. Tschudy (1939) also reached the same conclusion as a result of his studies on *E. telmateia*.

Bower (1908) and Browne (1927) regarded the sporangiophore as a modified branch and consider it to be axial in nature.

Hirmer (1933), Zeller (1893), Seward (1898) regard the sporangiophore to be a *ventral* lobe of a dorsiventrally split sporophyll. The sterile dorsal lobe has disappeared.

The consensus of opinion, however, favours its foliar nature, *i.e.*, the sporangiophore is a modified leaf.

GAMETOPHYTE

Germination of the Spore. The haploid spores germinate [illegible] n viable from 5—20 [illegible] eriod. Medium light, [illegible] table for germination. [illegible] ty to the thick spore [illegible] igh rate of respiration [illegible] itochondria present in the spores.

Jyotsana and Mohan Ram (1964) studied the germination of spores in *E. debile* (now called *E. ramosissimum* sub. sp. *ramosissimum*). The following account is based on their observations (Figs.

7·15, 7·16). They studied the germination in Moore's Medium. It took two to three days for the spores to start germination.

Prior to germination the large vacuole is replaced by several small vacuoles; the chloroplasts surround the nucleus. The spore [illegible] lle spore layer ruptures. The [illegible] The spore contents divide [illegible] e small lenticular primary [illegible] etophytic cell, [illegible] vhereas the pro- thallial cell has [illegible] The rhizoidal cell elongates into tl [illegible] The prothallial cell divides in various planes to give rise to the rest of the prothallus It usually divides by a transverse wall (Fig. 7·15, C—E)

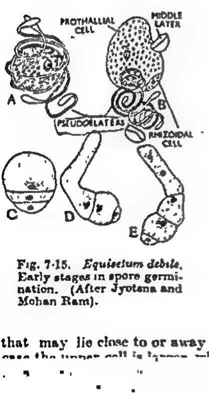


Fig. 7·15. *Equisetum debile.* Early stages in spore germination. (After Jyotsna and Mohan Ram).

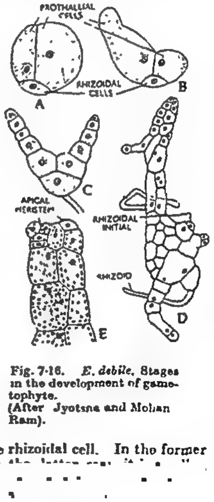


Fig. 7·16. *E. debile.* Stages in the development of gametophyte. (After Jyotsna and Mohan Ram).

that may lie close to or away from the rhizoidal cell. In the former case the upper cell is larger, whereas in the latter case it [illegible]

[illegible]

a flat green and leaf like expanse of tissue or to an elongated and branched thallus. Any superficial cell of the thallus at this stage

may divide unequally into a small **secondary rhizoidal cell** and larger cells. The former (Fig. 7·16) develops into a secondary rhizoid. Many such rhizoids may arise. Later the thalloid tissue increases in thickness by further anticlinal and periclinal wall into a bulky cell mass gorged with starch. Cell divisions later take place in all planes to form a cushion shaped massive thallus that is several cells in thickeness and bears numerous rhizoids on its lower surface. Earlier growth of the thallus is by a single apical cell, which is later on replaced by a group of meristematic cells (Fig. 7·16). Further development leads to the formation of a prothallus with three distinct regions :—

1. The spongy green upper part of erect green lobes.

2. The middle prostrate region of light-yellow colour.

3. The lowermost region of colourless cells that give off rhizoids.

The prothallus grows by means of a marginal meristem. The erect lobes develop by the activity of an inverted pyramid like **lobe initial** which divides by an oblique wall to form an **upper** and **lower cell.** The former develops into an erect green lobe and the latter divides to increase the thickness of the prostrate part. The upper cell divides by two transverse walls. The upper of these two divides by a longitudinal wall. The subsequent divisions may be transverse or both transverse and longitudinal and form a uniseriate or a multiseriate erect lobe.

As a result of the developmental changes described above three types of prothalli may develop :—

1. Light green male prothalli (Fig. 7·17, C).

2. Deep green female prothalli (Fig. 7·17, D).

3. Bisexual prothalli with their male branches and thick and fleshy female branches (Fig. 7·17, E).

A few deviations from the normal course of development were noticed by Jyotsna and Mohan Ram. These are :

(*i*) The prothallial cell may divide by a vertical wall (Fig. 7.17) and the two cell thus formed may divide by transverse walls to form two filaments or only one of them may *divide* further.

(*ii*) The rhizoidal cell grows into a primary rhizoid at a very late stage.

(*iii*) Sometimes the prothallial cell divides late after it has achieved a considerable size.

(*iv*) The meristematic cells may divide regularly to form a rounded prothallus or they may divide irregularly to form a prothallus irregular in shape.

Mature Prothallus (Figs. 7·17, 7·18, 7·19, 7·20.)

The mature gametophytes are dull brownish green thalloid structures generally found in abundance on the clayey soil along

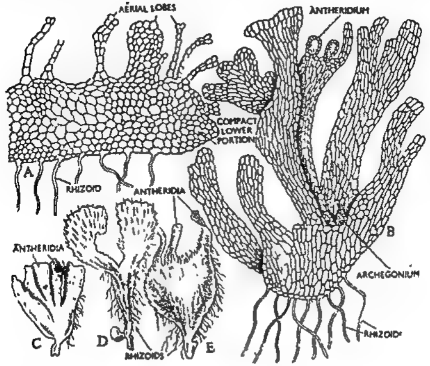


Fig. 7·17 (A—E). Prothallus of *E. debile*. A. L.S. of young prothallus. B. A bisexual prothallus showing a lower compact region bearing rhizoids and archegonia and upper spongy region bearing antheridia. C. A male prothallus. D. A female prothallus. E. A bisexual prothallus (C—E. After Jyotsna and Mohan Ram).

the banks of streams and rivers. They prefer shady places. They are definitely dorsiventral and grow in prostrate position on the surface of the soil without any sub terranean portion. Mature well developed prothalli of the foreign species are described as 'green pinheads'. They are usually 1-10 mm. in diameter but in *E. debile* the prothallus is very conspicuous reaching, when several months old diameter of 3 centimeteres. It becomes red in colour when growing in the bright light. The young prothalli look like small, green and red pinneads. The prothallus is semicircular in outline with an entire margin and a heavy cushion like central portion. Sometimes there is a notch at one side (posterior). As stated above green irregularly shaped lobes or plates arise from the upper surface and the marginal regions of the prothallus (Fig. 7·17). Numerous ... walled, hyaline, uni
underside of the cent

tophyte to the substratum. The entire margin of the cushion is meristematic in nature.

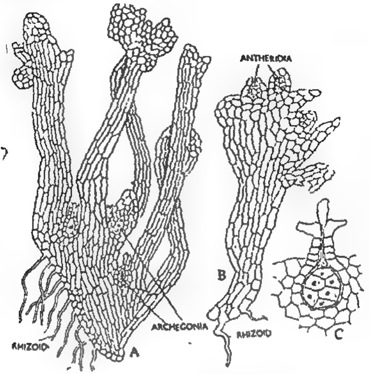


Fig. 7·18. *E. arvense.*
A. Female prothallus bearing archegonia.
B. A male prothallus bearing emergent or projecting type of antheridia.
C. An archegonium with young embryo.

The prothallus is often attacked by a fungus in the upper cells of the lobes. Generally it is dorsiventral but in *E. debile* it is radial (Kashyap, 1924), heart-shaped and has meristem all round. It differs from *L. cernuum* in the absence of a cylindrical body.

ANATOMY OF THE PROTHALLUS

Internally the prothallus is differentiated into two well marked regions :

1. Lower or basal compact, rounded, parenchymatous portion forming the disc (Fig. 7·17, A).

2. An upper spongy portion.

Disc. It consists of a large celled parenchymatus tissue without any air spaces between them. The cells are usually all alike. They lack chorophyll and are full of starch grains The chloroplasts which were present in the whole body of the prothallus in the earlier stages have all been transformed into leucoplasts. This

transition is gradual and starts from the cells in the lower region whereas the [illegible] are green [illegible] the diameter [illegible] cells of the c[illegible] tion and also the sex organs.

Spongy upper portion. It consists of densely crowded green vertical lobes [illegible] The lobes ar[illegible] tissue several [illegible] and thinner, [illegible] They are eith[illegible] are arranged in a compact manner so that the spaces between them are narrow and the prothalli appear to be solid. In other cases the lobes are open and the prothalli appear to be spongy. This is the case when the prothalli grow in moist places.

SEX ORGANS

In most species (*E. laevigatum*, *E. giganteum*, *E. telmateia* etc.) [illegible] ical [illegible] the [illegible] 31; [illegible] ood [illegible] *E.* [illegible] bear male sex organs, whereas under favourable conditions some prothalli are persistently male and others are female first and later bear male sex organs. Castle [illegible] *arvense* and found [illegible] at a later stage [illegible] be recognised quite early during their development, *i.e.*, even before they bear sex organs. The male prothallus is small and the part bearing the antheridia is more or less folded. The female prothallus is larger of the two. The male prothalli are yellowish to reddish as contrasted to the green female prothalli. The colour of male prothalli is due to the presence of orange-red pigment which develops in the chloroplasts of the antheridial jacket cells (Hauke, R.L, 1972). In other species where the gametophytes are monoecious the prothalli are invariably female in the beginning and even smallest ones bear archegonia but later on they produce antheridia, *e.g.*, *E. debile*. Joyet-Lavergne (1926-34) found that in some species of *Equisetum* (*E. arvense*, *E. maximum*, *E. limosum*) there are two

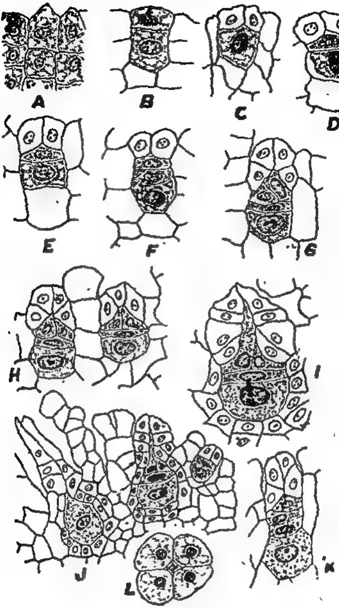


Fig. 7·19 (A—L). *Equisetum debile.*

A. Showing archegonial initial. B. The initial has divided into an upper primary cover cell and lower central cell. C. The cover cell has divided by two intersecting walls into 4 neck cells. D. The central cell has divided into primary neck canal cell and ventral cell. E. Same as D. F. Showing neck canal cell, ventral canal cell and egg. G. The neck has become 8-celled and neck canal cell has divided by an oblique wall into two. H. Archegonia with two neck canal cells lying side by side. I. Fully developed archegonium with two boot-shaped neck canal cells lying side by side. J. V.S. thallus showing three archegonia at various stages of development. K. An archegonium with two ventral canal cells. L. T.S. archegonium through neck region showing a tier of 4 cells.

(All after Jyotsna and H.Y. Mohan Ram)

categories of spores based on their physico-chemical reactions.
ied
ory
B
ral
dyes than the latter.

Archegonia (Fig. 7·19). They develop on young prothalli
obes are beginning to
are usually found near
prothalli they become
surface of the pro-
ertilisation of the first

Structure The mature archegonia (Fig. 7·19, I, J) have the
protruding.
or 4 cells in
ricate (bent
ening for the
entry of the ... The axial row consists of the egg cell, the ventral
can ... the number of the neck
can ... are "boot shaped" (Fig.
7·19, I). At maturity there is the usual gelatinisation of all axial
cells but the egg.

Development (Fig. 7·19).

cells (Fig. 7·19, C, D). Each of these divides transversely to form an
... 3 or 4 cells in height (Fig. 7·19, G, H). It projects
ll divides transversely
tral cell (Fig. 7·19,
the primary canal
nto two 'boot shaped'
neck canal cells (Fig. 7·19, H, I) by a vertical division (*E. debile*, *E. arvense*, *E. hyemale*, and *E. limosum*). Kashyap (1914) reported
only one canal cell in *E. debile* ...
shaped cell lying side by side.
a transverse division into a ...
Jyotsna and Mohan Ram (1968)
primary neck canal cell, in *E. ramosissimum*, into two boot-shaped
neck canal cells. They also observed archegonia with two ventral
canal cells (Fig. 7·19, K).

The last step in the archegonial development is the usual gelatinisation of the neck canal cells and the ventral canal cell. No embryo is found on any prothallus before the end of December. Thus all archegonia produced before that time are unfertilized.

Antheridia. Th[illegible] is several months old and is large[illegible] margins. Th[illegible] part of [illegible]phyll. In [illegible] them

1. The embedded type.
2. The projecting type.

The embedded type develop on the lower massive and cushioned part of the prothallus. The projecting type usually develop in starved prothalli and are found at the apices or margins of the erect lobes. Both the types are similar in structure and develop[illegible] initial is [illegible] ll of the [illegible] initial. [illegible] as the

Development of Antheridia

A. **Embedded type.** The embedded type of antheridium develops from a superficial cell cut off by the marginal meristem (Fig. 7·20, A). The younger antheridia lie nearer to the margin and the older towards the centre. The antheridial initial divides by a periclinal wall into an outer **primary jacket initial** and an inner **primary androgonial cell** [illegible] 20, [illegible] ja[illegible] diff[illegible] several times to form a group of [illegible]—G) which divide further and form [illegible] 7·20, H) There are usually 256 such [illegible] a centrally placed nucleus surrounded by chloroplasts which later on disintegrate Two **blepharoplast** granules [illegible] morphoses into a multiflagellate spermatozoid (Fig. 7·20, A—J).

B. **Projecting type.** [illegible] marginal [illegible] antheridial initial [illegible] primary wall cell [illegible] primary androgonial cell [illegible]

embedded type. The number of androcytes formed in this case is smaller than in the embedded type.

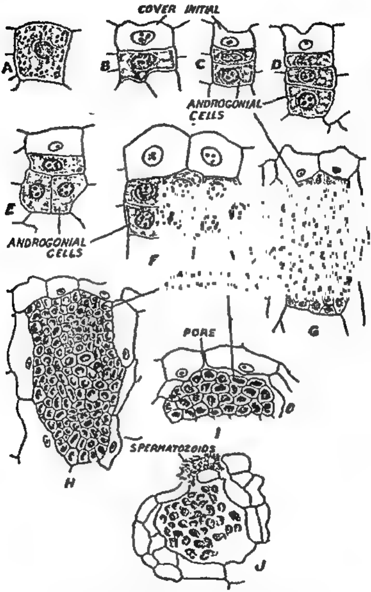


Fig. 7 20. *Equisetum debile.*

A—H. Stages in the development of an antheridium.
I. J. Mature antheridia showing dehiscence.
(After Jyotsna and Mohan Ram).

Spermatozoid. The androcyte metamorphoses into a spermato-

blepharoplast is regarded by Sharp (1912) to be composed of a number of granules. These granules fuse to form a continuous thread (Fig. 7·21, G, H). The nucleus shifts to one side of the androcytes and elongates and becomes curved (Fig. 7·21, G, I). One end of the

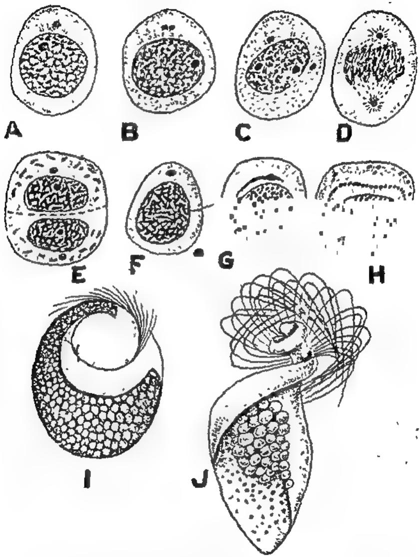


Fig. 7·21. (A—J). *Equisetum*. Spermatogenesis.

A. Sperm mother cell with a dark staining body in the cytoplasm. It is the blepharoplast. B. Division of the blepharoplast. C. The bodies seprate. D. *Blepharoplasts* at poles of the spindle. E. Two *androcytes formed.* F. G. H. Fragmentation of blepharoplast in the androcyte. I. Nucleus and blepharoplast become spirally coiled. J. Mature sperm. (After Sharp)

nucleus is next to the blepharoplast (Fig. 7·21, G, H). The nucleus now elongates considerably and becomes spirally coiled (Fig. 7·21, I).

The blepharoplast thread also coils spirally. Later numerous flagella

... three ... motor ... stalk. vesi- ... It absorbs water and increases in size. Major portion of the spermatozoid is made up of nucleus and blepharoplast. Cytoplasm also envelops the entire spermatozoid.

Mature antheridium. The mature antheridium is a more or less globular structure. It is s... the lower massive cushion like part of ... borne on the margins or apex of th... antheridium consists of a single la... The jacket may consist of 3—5 cells. ... spermatozoids (Dracinschi, 1930).

Hauke (1963) studied the method of dehiscence of the antheridium and release of spermatozoids. His studies reveal that presence of water is essential for dehiscence. The cells around the antheridium absorb water by osmosis and enlarge. Water is also absorbed

...

Mohan Ram (1968) observed the formation of a lenticular opening due to the pressure exerted by the swelling of the mucilage surrounding the cytoplasm.

Fertilization (Fig. 7·22). Water is essential for fertilization. As a result of disorganisation of the axial row of cells of the arche-... ...ed ... gg- ... nt ... er- ...

cell in *E. debile*. Many archegonia

Kashyap (1914) observed as many as 15 embryos on one prothallus in *E. debile*. This is quite contrary to other vascular cryptogams where only one embryo develops on one prothallus. Kashyap

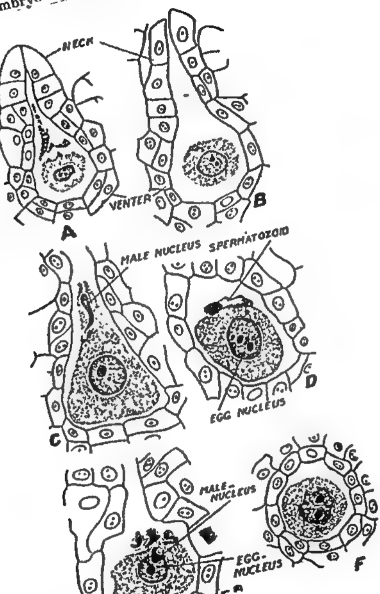


Fig. 7.22. *Equisetum debile*.
A. A mature archegonium. B. Archegonium with open neck. C—F. Stages in fertilization. (After Jyotsna and Mohan Ram)

observed two hundred archegonia on a prothallus of *E. debile*. Most of them contain young embryo but only a few are able to reach maturity.

DEVELOPMENT OF EMBRYO

f the sporophyte. It

de[illegible] l venter, which grows

int[illegible]

cal[illegible]

neck is also seen to persist in some species (*E. arvense*). The detailed embryology of *E arvense* is described below:—

[illegible]

epibasal [illegible] by pobasal cell. There is no suspensor. The epibasal cell lies nearer to the archegonial neck. Both the cells divide by a longitudinal wall to form quadrants [illegible]

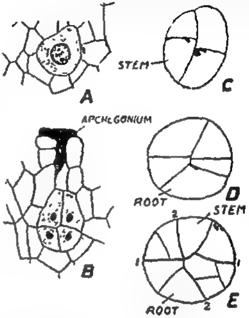


Fig. 7·23. (A—E). Earlier stages in the development of embryo in *E. arvense.*

[illegible] by three intersecting walls enclosing a central tetrahedral cell which functions as [illegible] apical cell. The [illegible] leaf initials [illegible] remain fused to [illegible] ap (1914), Sethi [illegible] apical cell does not divide in a regular manner to cut off leaf initials but the cells ly-

[illegible]

logy in *Equisetum* is exoscopic.

[illegible] towar[illegible] stem [illegible] leaf initials form the first leaf sheath. The root grows slowly and pierces through the underlying prothallus tissue and grows into a

small and short-lived first or **primary root.** The stem apex divides actively and grows out after piercing the calyptra. Second and third leaf sheaths arise from the nodes of the young stem and give it a characteristic jointed appearance. Other leaf whorls arise at regular intervals on the stem. The later formed leaf sheaths have 4—7 leaves. The primary stem grows in air, turns green and stops growing after forming a few nodes and internodes (Fig. 7·26, A—F). Later a secondary branch arises from its base (Fig. 7·26, A—F). It grows to form 10—15 nodes and internodes and stops growing. Like this tertiary and quaternary shoots arise and grow to a limited extent in the air. Ultimately one of the shoots instead of growing erect [illegible]

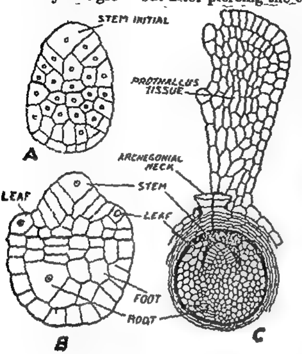


Fig. 7·24. Embryology in *E. arvense*. (After Sadebeck)

[illegible] **rhizome.** [illegible]

endogen[illegible] plant. [illegible] *E. palustre* and *E. telmateia.*

In *E. debile* the first wall of the oospore is vertical (Fig. 7·25, A) and the second is transverse. In this species the shoot, leaves and root initials arise in the epibasal half. The root initial differentiates quite late from one side of the lower half of epibasal region. The hypobasal region develops into a bulbous foot. The rest of the stages are similar to *E. arvense*. *E. hyemale* is similar to *E. debile.*

Morphological and anatomical studies of *Equisetum* reveal to possess both hydrophytic and xerophytic characters. The hydrophytic characters are :—

1. Presence of vallecular canals in the cortex.
2. Presence of carinal cavities in the vascular bundles.
3. Less developed xylem. 4. Hollow pith.

The xerophytic characteristics are ; 1. The rhizome is deep seated.

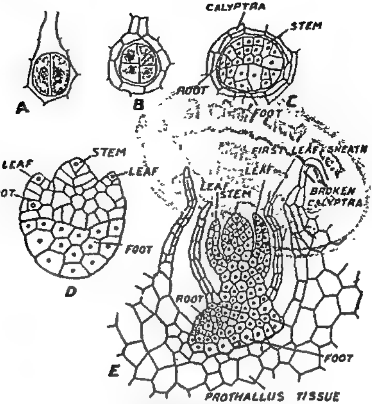


Fig. 7 25. (A—E). *Equisetum debile.* Various stages in the development of embryo.

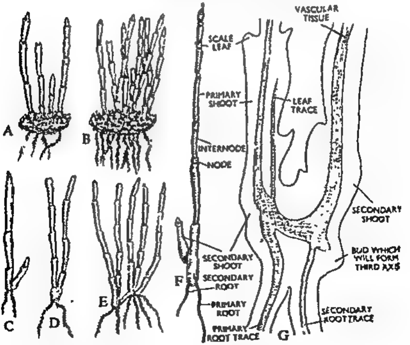


Fig. 7·26. Sporophytes of *Equisetum debile* (A—E) and *E.* (F—G)

F. A. young sporophyte *of E. arvense* with primary and shoots. G. A. diagrammatic L. S. through young sporophyte mary and secondary shoots. Note the vasculature.

2. The stem ... ..ridges and grooves. 3. The stem has sunken stomata. 4.

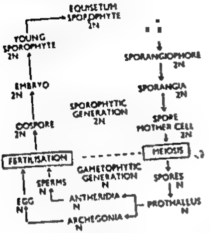


Fig. 7·27. A graphic life sketch of *Equisetum*.

sence of well developed ... and chlorenchyma.

The habitats of various species are in accordance with their structures. Most of them live in moist soil apparently their ancestral habitat, but some have become adapted to dry localities though still maintaining the hydrophytic structures.

Classification of the Genus. The genus has further been classified into two subgenera. These are: (*i*) sub-genus *Equisetum* and (*ii*) sub-genus *Hippochaete*. *Equisetum* includes species in which the stomata are not sunken and are in level with epidermal cells, *e. g.*, *E. sylvaticum*, ... *E. limosum*, *E. palustre*, etc. In these species the strobilus does ... of the axis, but it bears sporangio- ... obilus is, therefore, rounded. The ... ands. In *Hippochaete* the stomata ... not scattered. They are always ... roject slightly beyond the sporan- ... ecies included in this sub-genus are ... mosissimum, *E. laevigatum* etc

CHAPTER VIII

FILICOPHYTA OR PTEROPHYTA

Introduction. The filicophyta are an assemblage of vascular cryptogams that have established themselves most successfully to life on land. Their successful invasion of the varied habitats, their diverse habit, their supremacy in vegetative propagation and their remarkable success in competition with the modern seed plants [illegible] highest point in [illegible] comprise about [illegible] that have spread right from the equator to the arctic regions. The Indian hills [illegible] will add tremendously to this [illegible] known as the 'ferns'. — Post Carboniferous period

Geological records reveal that the ferns first appeared in the [illegible] ies. They dominated [illegible] d which has been des- [illegible] fern-like plants have [illegible] therefore, not justifi- [illegible] Rather ferns were in [illegible] opods and the seed [illegible] ter number in the modern age. Many of the modern families of the filicophyta had their representatives in the Mesozoic times especially the Triassic and Jurrasic periods. The Polypodiaceous filicophyta that are regarded as recent ferns, also had their representatives in the early Coenozoic.

Distinctive Characters. The filicophyta differ from lycophyta in possessing large and megaphyllous leaves. The leaf lamina is traversed by prominent and branched veins. The leaf traces and branch traces leave distinct gaps in the vascular organisation of the stem [illegible] means. [illegible] function [illegible]

from 2—5 cm. in *Anogramma leptophyla* to large tree ferns of *Cyatheacea* and some other families. Many love shaded and humid environments, a few like *Ceratopteris, Marselia, Salvinia, Azolla* are aquatic; some are xerophytic, *e.g.*, *Woodsia*. Hundreds of species are epiphytic (*Polypodiaceae*, some *Davalliaceae*, some *Aspleniaceae*) The rhizomes may be creeping, upright or grow above the soil into columnar aerial stems. In many ferns, *e.g.*, *Stenochlaena* the stem is weak and climbing attached usually by adventitious ... (*Pellaea*, *Dryopteris*, P ... to leaf inse ... branches in *Pteris* and *Pteridium* ... or palmate compound or highly dissected ... chotomously branched in some ... in many genera *e.g.*, *Pellaea*, ... be dichotomous or reticulate. ... tterns of venation in the ferns. ... sori and arise in groups from ... placenta. The sori are pro... indusia ... false. The sporangia in most ... annulus ... stomium. The sporangial development may be **eusporangiate** or **leptosporangiate**. Majority are **homosporous**, but a few like *Salvinia, Azolla, Marsilia, Pilularia* and *Regnelidium* are **heterosporous**. The fern *Platyzoma microphylla* has recently been shown to exhibit a condition of incipient heterospory (Tryon, 1964). The gametophytes may be **endosporic** or **exosporic**. In the homosporous types they are ... The antheridia ... in the ... other ... pensor.

Anatomically the stem exhibits complex structure and ranges from a simple or a highly dissected protostele, or a siphnostele or a dictyostele to polycyclic conditions (see under stelar system). The development of leaf traces and leaf gaps make the stem anatomy complex. The xylem lacks vessels except in *Pteridium aquilinum* and *Marsei*... almost a constant pattern of ... ina and the petiole show a great amount of variation ... l structure.

VEGETATIVE PROPAGATION

The ferns reproduce vegetatively by the following methods :

1. **Fragmentation.** It is of common occurrence among ferns with creeping axis or the rhizome. The older parts of the rhizome decay. When the progressive rotting of the older portions reaches beyond the branches, the latter separate and act as independent plants. Each branch has its own apical cell and is secured to the soil by adventitious roots. It grows into a new plant. The best examples are *Pteridium aquilinum, Dryopteris rigida, Pteris* and *Adiantum*. In some species of *Dryopteris* the rhizome splits into

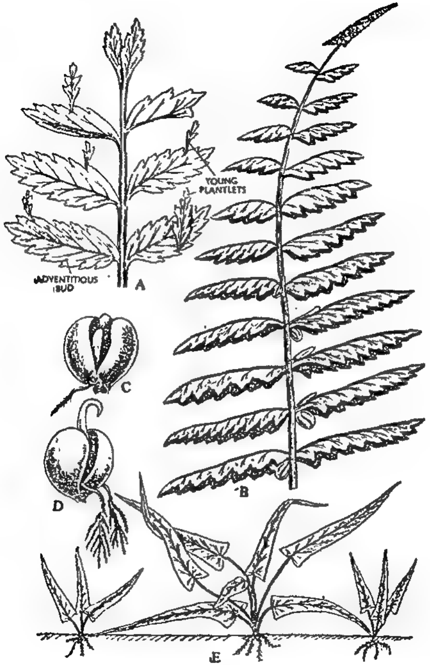


Fig. 8 1. Methods of vegetative propagation in ferns. A. *Asplenium viviparum* showing marginal adventitious buds that have grown into young plant lets on the pinnae. B. *Cystopteris bulbifera*: Portion of a leaf showing pinnae bearing adventitious buds on their bases. C—D. Germinating buds as in B. E. *Camptosorus rhizophyllus*: Vegetative propagation by means of drawn out leaf apices.

segments by the decay of intervening cells. This is a very quick and an efficient method of vegetative propagation and is responsible for the gregarious habit of certain ferns.

2. **By the format**[illegible] develop adventitious bu[illegible] vegetative propagation. [illegible] on the underside of the lamina. *Asplenium viviparum* (Fig. 8·1, A) and *Diplazium celtidifolium* develop them on the upper surface of the leaf lamina. In both cases the buds appear to be marginal in the first instance. In *Cystopteris bulbifera* they develop at the [illegible] *Wood-* [illegible] mme- [illegible] venti- [illegible] lants. [illegible] *situ* (*Asplenium viviparum*).

3. **Embryonic Leaf Apices.** In *Camptosorus rhizophyllus* (Walking fern) the long and simple leaves have drawn out and taper- [illegible] out leaf tip comes in contact [illegible] ous bud. During germina- [illegible] the soil and gives rise to [illegible] e sporophyte thus formed [illegible] by the rotting of the narrow upper part of the leaf. Embryonic leaf apices in *Asplenium pinnatifidum* and *Polystichum rhizophyllum* also produce new plants in the same fashion. In both the cases the leaf tips are drawn out.

[illegible] **Tubers.** In some species of [illegible] egular tuberous bodies are [illegible] lateral branches store food material in the form [illegible] pearance. They are [illegible] structures are called [illegible] drought. They pers[illegible] vent of favourable periods they germinate into new plants. They serve the dual function of perennation and vegetative propagation.

5. **By** [illegible] In some ferns (*P.* [illegible] develops direc[illegible] can grow into a new plant. In *Ophioglossum* [illegible] *O. pendulum* and some other species adventitious buds Fig. (8·2) appear on the roots. These buds originate from one of the superficial cells cut off by the apical cell (Rostowzew). Such buds can develop into new plants and are an efficient means of vegetative propagation. They help the plants to overwinter and to propagate them vegetatively. Wardlaw (1953) stated that in *O. vulgatum* the root buds may originate from segments of the apical meristem "or they originate endogenously in the middle cortex." A group of cells or sometimes in-

[illegible] ...d meristematic. They [illegible] The first leaf and shoot [illegible] ...lso appears. *Ophioglossum* reproduces mainly by this method.

The phenomenon of Apogamy has been dealt in detail in Chapter I.

STELAR SYSTEM IN VASCULAR CRYPTOGAMS

Stelar Theory. Sachs (1875) formed an idea that the vascular system of the plant body is a continuous system. This idea was introduced with a greater emphasis by Van Tiegham and Douliot in 1886. They proposed and developed the **Stelar theory** according to which the root and the stem are fundamentally similar in gross anatomy, because in both the cortex encloses the central part of the axis. The central part or the core of the axis is called the stele. *So a stele (Greek word meaning column) is the core of the axis which includes the vascular system, the interfascicular portion, the pith (if present) and some surrounding portions of the fundamental tissue in the vicinity of the vascular bundles (pericycle).* This concept of the stele as proposed by Van Tiegham and Douliot was widely accepted by the plant morphologists and plant anatomists. The term stele is restricted only to the primary vascular tissue.

The concept of the stele, its classification and nomenclature have undergone many changes since it was proposed in 1886. It is very difficult to apply the original definition of the stele in the case of most of the seed plants, as there is no clear cut demarcation between the cortex and the stele. Van Tiegham (1886) regarded the endoder- [illegible] ...he stele. Endoder- [illegible] ...boundary between the stele and the cortex in the stems and roots of many vascular cryptogams. [illegible] ...present in the stems of many [illegible] ...and pericycle are absent. [illegible] ...ifford, 1962; Esau, 1953) to discard the term stele [illegible] ...and replace it by the term vascular cylinder [illegible] So the modern usage of [illegible] ...nts, means the vascular cylinder alone. In the vascular cryptogams where there is a clear demarcation between the central cylinder and the cortex, the term stele can be used in the real sense of its definition.

It may, however, be stated here that although the endodermis may not be morphologically distinct in many seed plants, yet physiologically its presence cannot be denied in the seed plants. There is always a layer whose physiological activities (chemical reactions) are certainly distinct and different from all the other layers or its neighbouring layers. The name **endodermoid layer** has been suggested for such a layer of physiologically distinct nature by Esau (1966).

The second debatable question is the nature of the [illegible]

vascular cylinder in the filicophyta (ferns) and the seed plants. In these plants the large leaf traces seem to play a prominent role in determining the vascular organisation of the stem. Wardlaw and Wetmore (1951) and also Wardlaw (1946) consider these large leaf traces in the megaphyllous vascular plants as distinct units of structure and regard the stele or the vascular cylinder of the stem as a composite structure. According to them the stem stele is made up of both foliar (leaf) and cauline (stem) vascular elements The ratio between the two types of elements constituting the stem stele no doubt varies with plants. Wetmore (1953), however, regards that in some ferns the entire vascular organisation of the stem is foliar in nature. It has no doubt been shown (Wardlaw, 1944) that in *Dryopteris dilatata* "the incipient vascular tissue originates in contiguity with the active meristems of shoot, buds, leaves and roots". The distinguishing vascular strand of the young leaf primordium, at the shoot apex, becomes united with the complete vascular cylinder of the stem. There are no leaf gaps at this stage. But lower down, *i.e.*, as we proceed towards the mature parts of the stem, small leaf gaps begin to appear at the points of insertion of the leaf trace on the stele of the stem. These small **leaf gaps** enlarge in size with the enlargement of leaf trace bundles. Since the leaves are arranged in close spirals on the mature stem, the stele of the stem becomes broken by the overlapping leaf gaps and appears dissected These observations indicate that there is a close relationship between the stelar organisation of the stem and the enlargement of the leaves. The formation of the leaf gaps has been explained by Wardlaw (1968) in his own words "An anatomical analysis also shows that, in growing leaf bases, there is avery considerable tangential enlargement, due chiefly to an increase in the volume of the cortical and medullary parenchyma. Concomitant with these developments, the leaf trace which is initially a crescentic mass in cross section, is pulled apart into four or five separate strands, with parenchyma in between. In brief, the distribution of growth in the leaf base is such that the initially crescentic vascular trace is disrupted by being subject to tensile stress. The cylindrical, still undifferentiated stele of the shoot is also affected by this tensile stress and hence the formation of the leaf gaps."

It is evident from the above description that changes in the stelar organisation of the shoot are brought about by the appearance of leaf traces and leaf gaps. Wardlaw suggested that these changes can be stopped by defoliation of the shoot apices. He (1944, 1949) conducted experiments on certain ferns (*Dryopteris dilatata, D. filix-mas, Angiopteris evecta, Onoclea sensibilis, species of Osmunda* and *Todea*) by removing the young leaf primordia at the apices of the shoots He obtained the desired results with *Dryopteris dilatata* and *D filix-mas*. In both these cases the young leaf primordia were removed from the shoot apices. Normally the stems show a dictyostelic condition (Fig. 8 5 E). Under experimental conditions, *i.e.*, when leaf primordia were removed, the stem in that region showed solenostelic stelar organisation. Even protostelic condition was also obtained by such experiments. These experi-

ments show that the stelar organisation of the stem in the filicophyta is dependent, to a greater degree on the presence or absence of leaves.

In the microphyllous vasculai cryptogams (*Selaginella, Lycopodium,Isoets*) the leaf traces do not leave any leaf gaps in the stem stele, which therefore uremains ndisturbed. In these cases the vascular system of the leaf has no bearing on the stem stele

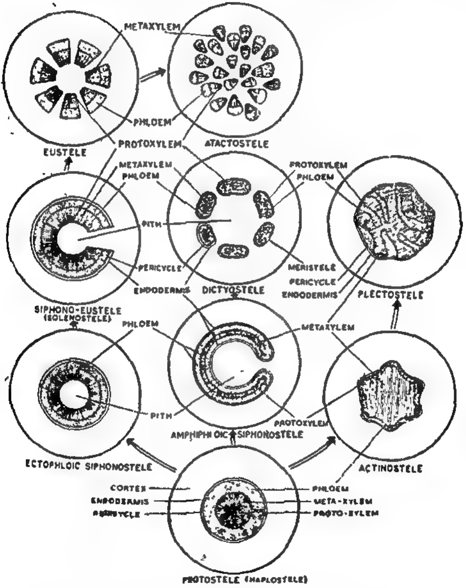


Fig. 8·2. Various types of stelar organisation in the vascular plants. (After Zimmermann)

Types of steles. Esau (1953) and Smith (1955) recognise two principal types of stelar organisation among the vascular plants. These are : (A) **the Protostele**, and (B) **Siphonostele.**

A. **The Protostele.** It is the simplest and the primitive type of stele. In this case the vascular cylinder consists of a solid core of xylem surrounded by phloem, pericycle, and endodermis (Fig 8·2). There is no pith The name **protostele** was suggested by Jeffrey (1897, 1899, 1902) and is regarded as a fundamental stelar type of the vascular plants from which the other type originated in the course of evolution. Brebner (1902) classified the protostele into two.

(a) **Haplostele** (Fig. 8·2). In this type of protostele the central core of xylem is smooth and is surrounded by a uniform layer of phloem It was found in the extinct psilophytales like *Rhynia* (Fig. 2·2) and *Horneophyton*. In the living genera it is characteristic of many species of *Selaginella*, e g., *S. chrysocaulos*, *S. kraussiana*, *S. selaginoides* etc. In *S. chrysocaulos* the ribbon shaped (Fig 6 6, A) haplostele has two protoxylem groups, *i.e.*, it is diarch and exarch. In *S. kraussiana* there are two haplosteles (Fig. 6·6, B). Such a condition is called distelic as compared to monostelic condition in *S. chrysocaulos*. In *S. willdenovii* (Fig. 6·8) the condition is tristelic or even tetrastelic because in this case there are three or four haplosteles. In *S. selaginoides* (Fig. 6·5) the monostelic haplostele has metaxylem surrounding completely the protoxylem. This condition of xylem is called **mesarch**. Some ferns like *Gleichenia dichotoma*, *Cheiropleuria* and *Lygodium* have stems that maintain protostelic condition throughout the life of the plant. In the former case the xylem is composed of tracheids mixed with parenchyma cells.

(b) **Actinostele.** In this case the xylem core is not smooth an may be stellate or star-shaped (Fig. 8·2) as in *Lycopodium serratu* (Fig. 4·6, C) and in the upper portions of the stem in *Selaginella sel ginoides* (Fig. 8·5). It also occurs in *Psilotum* (Fig. 3·2). The extin psilophyte named *Asteroxylon* (Fig. 2 8) also possessed a star-shap actinostele. In *Lycopodium volubile* and *L. clavatum* the xylem ours in the form of parallel plates alternating with phloem plates (F 4·6). Such an actinostele has been named as **plectostele** by Z mermann (1930, 1938). In *L. cernuum* the actinostele consists of (Fig. 4·6) regular groups of xylem in a mass ele. actinostele is called mi

3. In *H. scabrum* the metaxylem ring is interrupted by par enchyma gap thus forming two arcs. The protoxylem lies embedde in the central parenchyma.

4. In *Trichomanes muscoides* the lower xylem arc and phloe are absent thus making a collateral bundle.

5. In *T. microphyllum* xylem is represented by a single trach eid.

6. In *T motleyi* there is no xylem at all.

In rhizome of *Ophioglossum lusitanicum* the basal portion is pro tostelic (haplostele), whereas the upper part is dictyostelic [Gewirt and Fahn (1960)] In many ferns with complicated stelar organisa tion the basal portions of the stem possess a protostelic organisation.

B. **The Siphonostele** (Fig. 8·2).

(*a*) **Origin**. Medullated protostele is called **siphonostele** It is characteristic of the filicophyta. During the development of si phonostele the central core of xylem is replaced by parenchymatou cells . . . appears in the cen tre. . . . e upwards of rhizo mes of certain ferns (*Anemia*, *Schizaea*) clearly reveal the develop ment of siphonostele. In *Aneimia phyllitidis* (Bower 1923) the stele at the base of the rhizome is a typical protostele (Fig. 8 3, A). The lea traces given out at this stage do not disturb the protostele and also do not interrupt the endodermis. Higher up the sections reveal the presence of a central pith (Fig. 8 3, B) enclosed completely by a ring of tracheids. In this case the whole vascular system is surrounded by endodermis during the development of pith. Similar develop mental studies in *Schizaea*, and in the sporelings of *Botrychium*, *Hel minthostachys*, *Osmunda* and *Gleichenia pectinata*, reveal that the vas-

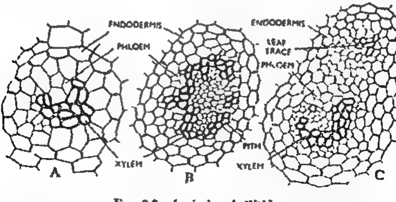


Fig. 8 3. *Aneimia phyllitidis*.

A. T S. near the base of rhizome showing protostele. B. T.S. at a higher level showing the appearance of pith C. T.S. showing siphonostele giving off a leaf trace without breaking the endodermis (After Bower)

cular cylinder is completely surrounded by endodermis during the development of pith. Gewirtz and Fahn (1960) conducted studies on developmental anatomy of *Ophioglossum lusitanicum*. They showed that the basal portions of the rhizome in this species possess a typical protostele. In the upper regions the stele is dicytostelic. In the transition zone below the level of the first leaf gap the pith appears in the centre. Gewirtz and Fahn (1960) showed that the pith originated from the xylem. Firstly, they observed the appearance of a few parenchyma cells mixed with xylem, Later the number of parenchyma cells increased gradually. These observations support the view that the pith i[illegible] intra[illegible] [illegible] intrastel[illegible] in [illegible] Boodle (1901), Gwynne [illegible] [illegible]homp-son (1920), and [illegible] of in-trastelar origin o[illegible] [illegible]central pith in *Botrychium virginianum*, *B. lunaria*, *B. ternatum* and *Osmunda regails* support the intrastelar origin of pith.

Bower (1923) stated that evidences of intrastelar origin of pith are also available from the study of fossil ferns. The ferns belonging to the families Botryopterideae and Zygopterideae of the carboniferous period illustrate the initial steps in this direction. In *Botryopteris forensis* the xylem forms a solid core. In *Diplolabis romeri* the xylem is composed of central zone of reticulated tracheids surrounded by a zone of pitted tracheids. In *Metaclepsydropsis duplex* the inner or the central [illegible] to form a mixed pith. [illegible] tion is found i[illegible] three steps which brought about intrastelarmedullation. These are:—(*i*) solid xylem core, (*ii*) heterogeneous xylem but without pith as in *Diplolabis*; and (*iii*) appearance of parenchyma in the central xylem core as exemplified by *Metaclapsydropsis duplex* and *Osmunda*

Jeffrey (1897, 1899, 1902, 1917) put forth his view that the pith is extrastelar in origin. He believed that pith originated as a result of invasion of the parenchymatous cells of the cortex into the stele. This he believed took place through the leaf gaps and branch gaps. He used the presence of inner endodermis between the pith and the vascular tissue as a proof of extrastelar origin of pith. According to him endodermis penetrated inwards together with the parenchyma of the cortex. This argument has been challenged by certain observations on *Selaginella* and *Pteridium*. In both these genera the endodermis has been proved to be stelar in origin. In *Pteridium aquilinum* Chang (1927) observed that endodermis, pericycle and protophloem arise from a common layer of procambial cells. Eames (1936) and Eames and Mac-Daniels (1947) have stated that pith is intrastelar in origin in some Lycopsida and ferns whereas in higher ferns it is extrastelar in origin.

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In the **amphiphloic siphonostele** ... *Dipteris, Platyzoma* ... m surrounds the xylem internally as well as externally.

In *Todea hymenophylloides* the inner endodermis appears as a discontinuous sheath There is no internal phloem.

Both the ectophloic and amphiphloic siphonosteles may occur in the form of a continuous cylinder of ... the leaf traces do not leave leaf gaps ...

... **Cladosiphonic si-phonostele,** ... d ... s named by Jeffrey as **Phyllosiphonic.** Both these types can be distinguished among ectophloic and amphiphloic siphonosteles. Appearance of leaf gaps in the siphonostele (phyllosiphonic) lead to a number of modifications. The leaf gaps are those parenchymatous regions that occur in the stele above the positions from where the leaf traces pass out from the central stele to the leaves. These leaf gaps or parenchymatous regions interrupt the continuity of the vascular cylinders

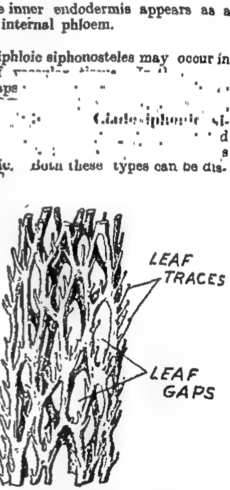

Fig. 8·4. *Dryopteris filix-mas.* Stelar organisation of rhizome showing a cylindrical network of interconnected vascular strands. It is a dictyostele.

If the stem or the rhizome bears leaves at distances the leaf gaps also appear at a considerable distance from each other. At such places the stele is interrupted and appears horse shoe shaped. The leaf trace appears as a small crescentic bundle (Fig. 8·2), *e.g., Adiantum pedatum.* The leaf gap closes at a higher level and the stele again becomes complete and circular. So the stele is perforated

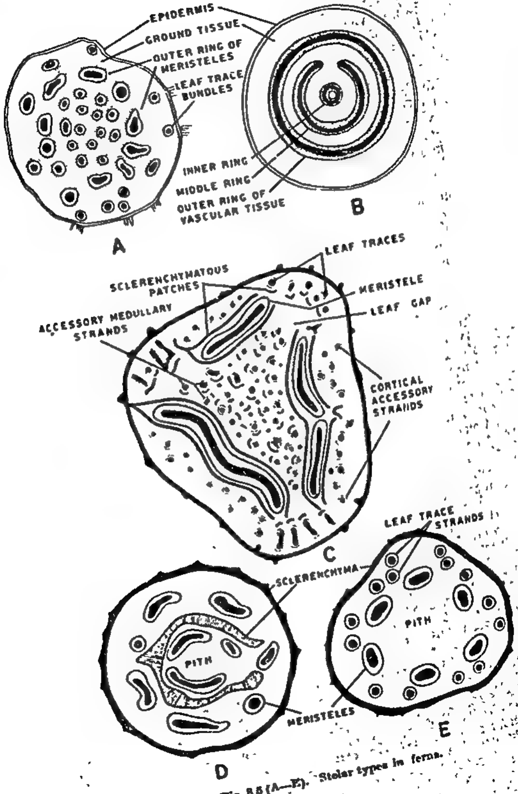

Fig. 8.8 (A—E). Stelar types in ferns.

A. Polycyclic dictyostele in *Platycerium aethiopicum*. B. Polycyclic stele in *Matonia pectinata*. C. Dictyostele in *Cyathea imrayana*. Note the sclerenchymatous strands around the meristeles and the accessory strands in the cortex and the pith. D. T.S. rhizome of *Pteridium aquilinum* showing dicyclic dictyostele. E. T.S. rhizome of *Dryopteris chrysocomo* showing dictyostele. (A after Lulham, B.C, after Bower)

... solenostele ... n ... c ... e

In a number of species of *Dryopteris* (*D. filix-mas, D. rigida, D. chrysocoma, D. erubescens*, etc.), *Pteris*, *Ophioglossum lusitanicum*, *Pellaea rotundifolia* and a number of other filicophyta, the rhizome is short and the leaves overlap each other. This leads to the overlapping of leaf gaps in the stele so that the lower part of one leaf gap is parallel with the upper part of another gap. Such an arrangement of the leaf gaps results in the formation of a cylindrical network of (Fig. 8 4) interconnected vascular strands. A cross-section of such a stele revelas the presence of separate vascular bundles (Fig 8·5, E) separated by parenchymatous patches. Each such vascular bundle is of concentric type and consists of a central core of xylem surrounded by phloem, pericycle and endodermis (Fig. 8 5, E). Individually these bundles are called the meristeles. Anatomically the meristeles are amphicerebral bundles with exarch, mesarch or endarch xylem. Such a siphonostele is termed as a dictyostele (Fig. 8·5, A, C, D, E). It is derived from the amphiphloic siphonostele.

Appeara ... onostele results in ... vascular bundles ... called **eustele** and is characteristic of seed plants (Fig. 8·2). Like the dictyostele the vascular strands in the eustele are also interconnected. In some cases the vascular strands are scattered and such a stele is called **atactostele** (Nast, 1944; Esau, 1953). It is found in the monocotyledons (Fig 8·2). Sometimes the vascular bundles in the eustele are bicollateral (cucurbitaceae, solanaceae), *i e.*, phloem is present on either side of the xylem (externally as well as internally). Such a condition is believed to be a 'secondary specialisation'. It should not be regarded as a relic of the primitive structure found in the filicophyta.

... medul... lary ... per... forations.

In some filicophyta ... *Marattia*, two or ... sent. Such a ste... *num* (Fig 8·5, D) there are two concentric circles of vascular tiss

The outer circle is composed of a number of meristeles, *i.e.*, it is dictyostelic. The inner circle consists of only two meristeles. Two patches of sclerenchyma of the ground tissue are present between the two circles of meristeles. Polycyclic stele in *Pteris elata* var. *karsteniana* consists of a larger number of meristeles in the inner ring than in the outer ring. In this case there are no sclerenchyma patches. There are three concentric rings of vascular tissue in *Matonia pectinata* (Fig. 8.5, B). Each ring has a typical solenostelic structure (Fig.8.5). Four concentric cylinders of vascular tissue have been recorded in *Pteris podophylla* (Bower, 1923). All the four are siphonostelic in nature In *Platycerium aethiopicum* there are four or more irregular concentric circles of meristeles (Fig. 8·5, A).

The anatomical study of the stems in dendroid Cyatheaceae reveals a still more complex vasculature. Transverse section through the stem of *Cyathea imrayana* (Fig 8 5, C) reveals the presence of broad meristeles that are enclosed with in broad plates of sclerenchyma. The leaf traces arise as number of strands that run obliquely through [illegible] leaf trace arises from the lower mar- [illegible] to this vasculature a number of [illegible] in the pith and the cortex. Each one of them is surrounded by endodermis and is often accompanied by a sclerenchymatous band. These cortical and medullary strands may anastomose freely and end blindly during their course downwards Some of them have also been noticed (De Bary) to pass out along with the leaf traces and enter the petioels. These vascular strands are considered to be the **accessory strands** that have originated in the pith or the cortex without any connection with the general vascular system. Such accessory strands have also been reported in the pith of *Hemitelia setosa* and *Ceratopteris thalictroides*.

Sporne (1962) uses a different nomenclature for the stelar organisation in the vascular cryptogams. He regards the ectophloic siphonostele as *medullated protostele*. The term *solenostele* has been used for amphiphloic siphonosteles and such siphonosteles that are perforated by leaf gaps at considerable distances. Sporne has not used the term siphonostele for the pteridophytes. The term *dictyostele* i[illegible] and the solenostele is much dissoc[illegible] are of the following types [illegible] tostele ; (*iii*) solenostele; [illegible]

Evolution of the Stelar System (Fig. 8·2). The consensus [illegible] that protostele is the [illegible] stelar [illegible] and is [illegible] (Fig. [illegible] The [illegible] ssessed [illegible] phyton, *Asteroxylon* (Fig. 2·8), *Psilophyton*, *Zosterophyllum*, etc. [illegible] resence of exclusively protostelic stems in the earliest vascular plants and

their retention in some of the living vascular ...

... actinostele ...

... plectostele ...

Another very important ... the protostele ... tion of the prot... the protostelic ... complicated stelar type ... ously by various auth... theories have been put forth to accord for its origin. These are the **intrastelar theory** and the **extra-stelar or invasion theory.** These have been discussed in detail in the preceding pages Appearance of pith led to the conversion of the protostele into a new type of stele called the **siphonostele.** Elaboration of siphonostele also followed two courses of evolution:

(a) The appearance of pith resulted in the formation of ...

... nodes) by one leaf gap (Fig. ... lar cylinder remains complete. Such as stele is also called ...

... bundles are scattered, as in mor... **atactostele** (Fig. 8·2).

(b) During another line of evolution the medullation of the protostele was followed by the appearance of phloem on either side

of the xylem and likewise internal pericycle and endodermis also appeared.
rounded by
xylem, ext
(Fig. 8·2).
stele (*Mar*
phonic.
leaf gap at
the leaf ga
Dictyostele
giate and leptosporangiate ferns the dictyostelic stems are protostelic at their bases. One such example is afforded by *Ophioglossum lusitanicum* (Gewirtz and Fahn, 1960). Recent experimental studies (Wardlaw, 1944, 1968) al

Polycyclic condition exhibited by some ferns like *Marattia*, *Matonia*, *Pteridium*, *Cyathea*, etc., also originated from the protostelic condition by further elaboration. This is borne out by the fact that in *Matonia pectinata* there is a regular transition from protostelic condition to solenostele and then to a polycyclic condition. The stem is protostelic at the base, then becomes solenostelic and ultimately

primitive condition.

Bower (1923) while discussing stelar organisation in the ferns outlined five steps that led to the elaboration of the protostele. These are:

(1) A solid xylem core or the protostele.

(2) A heterogeneous xylem, but without pith.

(3) A central pith surrounded by xylem ring.

(4) Interruption of the stele by a leaf gap or by overlapping leaf gaps.

(5) Appearance of internal phloem and endodermis.

All these steps are exemplified by both living and extinct ferns.

A number of recent workers have presented a different interpretation of the evolution of stelar system in the seed plants. They

eustele in these originated directly from the **protostele** through longitudinal dissection, without any intervening siphonostelic stage. Such a mode of organistation of the primary vasculature in the woody angiosperms that are now living has been studied by Dormer (1945, 1946, [illegible] (1958) [illegible] absent [illegible] has now [illegible] (Takh- [illegible] view is [illegible] eustele [illegible] protostele [illegible]

Namboodri and Beck (1968) have put forth a new concept that parenchymatous areas may arise in the stele without having any connection with the leaf gaps. Such a conclusion is based on detailed study of the primary vasculature in gymnosperms and angiosperms (Slade 1971) and is against Jeffery's leaf gap concept (1971) for ferns.

The above view supports another new interpretation that the primary vasculature of the stem is **Cauline** and not **foliar**. The protostele is clearly axial, not a foliar structure. That this is true becomes very [illegible] psilophytes from which [illegible] ave evolved were leafle[illegible]

Usually primary vasculature of stem is considered to be foliar in nature (Esau, 1965 b; Philipson and Balfour, 1963 ; O' Neil, 1961 ; Nast 1944) ; but the above view of its cauline nature is at variance with this.

Leaf Traces and Leaf Gaps. A leaf trace is that part of the vascular cylinder that extends between the leaf base and the point where it merges with the vascular system of the stem. The number of the leaf traces associated with one leaf may be more than one. So leaf traces connect the vascular system of the leaf with that of the stem.

In ferns and the seed plants the portion, lying immediately above the point of divergance of leaf trace from the vasuclar cylinder of the stem, becomes [illegible]

[illegible]

pages.

Branch Traces and branch gaps. [illegible] have vascular connections with the m[illegible] that connect the vascular system of a br[illegible] branch traces. Similarly there are branc[illegible] areas in stem vascular system just abov[illegible]

gaps and the branch gaps are not actually breaks in the continuity of the vascular cylinder because the vascular tissue maintains lateral connection just above and below the gap

SPORE PRODUCING MEMBERS

The spores are produced within specialised structures called the **sporangia** The sporangia, in most of the living filicophyta, occur in small or large groups called the **sori** (singular=sorus) The sori are variously arranged on the margins or ventral surfaces of leaves or leaflets. Such leaves are called the **sporophylls.**

The leaves, in most of the filicophyta, serve a dual purpose of photosynthesis and reproduction. In the common ferns like *Adiantum Pteris* and *Dyropteris* any leaf or leaflet can bear sori on its under surface. There is no distinction between fertile and sterile leaves. All the leaves and their leaflets are potentially fertile and are capable of bearing sporangia. There are however some ferns which exhibit segregation of photosynthetic and reporductive functions The genus *Osmunda* affords a good example of cases where a few pinnae or leaflets of a leaf are set aside for bearing sporangia whereas the others are sterile and photosynthetic *Osmunda regalis* (Figs. 9·2, 9·3) has a pinnate compound leaf in which the upper or distal pinnae are fertile whereas the lower or proximal pinnae are sterile (Fig. 9·2). In *Osmunda claytonniana* (Fig. 9 1) and *O. javanica* certain pinnae, anywhere along the leaf, have smaller size and bear sporangia. These examples illustrate restriction of sporangiferous area in the same leaf. In *O. cinnamomea* the leaves are dimorphic, *i.e.*, there are two types of leaves (Fig. 9·4). There are : (i) sterile leaves that have well developed leaf blades and appear late in season, and (ii) fertile leaves that lack lamina and appear earlier in season. Other examples of this type are *Matteuccia struthiopteris* and *Blechnum spicant* in which the rhizome bears : (i) sterile leaves that are large and broadly expanded and (ii) fertile leaves or sporophylls that are attenuated and have reduced lamina. These two types of leaves occur in distinct alternating zones. In *Pellaea atropurpurea* (Fig. 8·10), the sterile leaves have oval pinnae and fertile fronds have narrow and elongated pinnae.

The Sorus. The term sorus has a Greek origin. It actually means a heap or a group. The group of sporangia is, therefore, called a **sorus.** A sorus may have from two to many sporangia. The sorus may be protected by a revolute margin or by a special [illegible] indusium [illegible] it may be unprotected and [illegible] s also includes the **receptacle** or the **placenta** on which the sporangia arise The indusium if present may also be regarded as a part of the sorus.

There are some ferns in which the sporangia are naked (without indusium) and occur scattered along the veinlets. They do not form sori, *e.g.*, *Leptopteris hymenophylloides*. In *Todea barbara* the sporangia are densely scattered and are not covered by an indusium. The sori in this case are ill defined. The sporangia in boh these cases

are superficial. In the living genera of the Marattiales the superficial sporangia are arranged in definite sori. In *Christensenia* the sori are naked, circular and are irregularly arranged between the lateral veins. In *Marathia*, *Angropteris*, *Danaea*, etc., the sori are elongated and are situated below the lateral veins. Among the polyopodiaceae the sori are naked in *Polypodium* and some other genera.

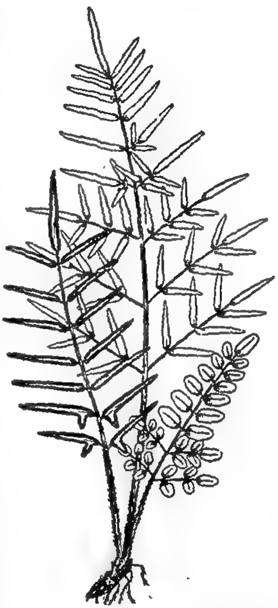

Fig. 8·6. *Pellaea atropurpurea*. A complete plant with one sterile frond and two fertile fronds. Note the pinnae in fertile fronds are narrow and elongated.

The ophioglossales are a group of interesting ferns in which the sporangia are marginal in position and are borne on fertile spikes that arise on ventral surface of a sterile lobes. The leaf, in the ophioglossales, consists of a petiole which bears a simple (Fig. 9.1) or a dissected sterile lamina from whose ventral surface arises a simple or a branched fertile spike. The fertile spike in *Ophioglossum* bears sporangia arranged in two rows (Figs. 9.1, 9.2). The sporangia are embedded and fused together. The spike terminates in a small sterile process. Every sporangium is supplied with a vascular trace. The fertile spike in *Helminthostachys* bears groups of sporangiophores arranged in many rows Each sporangiophore bears groups of sporangia and a few green scale like lobes at the tip. The spike in *Botrychium* is branched once, twice or many times. Each branch bears two rows of marginal sporangia. The sporangia in *Osmunda*, *Davallia*, *Trichomanes* and many other ferns are also marginal in position (Fig. 8.7, *A*). In *Osmunda* the fertile pinnae are bladeless, *i.e.*, have either reduced or no lamina. In *Schizaeaceae* the sporangia

isolated and are protected by a false indusium. They originate from initials that arise marginally, but get displaced to ventral side during development

In ·· ... sori on the ventral surface c ... ends or rarely along the middle of the ... ly by hair and scales There are no indusial flaps. The sorus consists of a single circle of sporangia.

In *Hymenophyllaceae* the sori are marginal and are characteristic in that the vein supplying the receptacle grows through it (by the activity of a basal meristem) and forms a long thin bristle, *e.g.*, *Trichomanes*. The sorus is protected by a cup-shaped indusium. The indusium is bilipped in *Hymenophyllum*.

The indusium in *Dicksoniaceae* consists of two flaps that form a box like structure in *Cibotiam barometz* The sori are marginal in position.

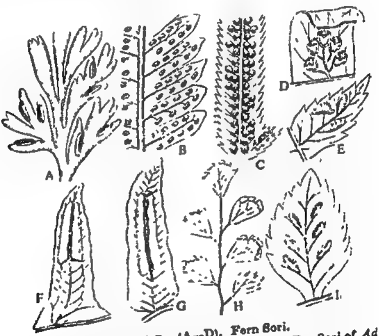

Fig. 8·7. (A—D). Fern Sori.
A. Sori of *Asplenium* with unilateral indusia. B. Sori of *Adiantum* covered by a reflexed margin of the pinnule. C. Sori of *Dryopteris* covered by reniform indusia. D. Sori of *Polystichum* covered by peltate indusia. E. *Aethyrium filix-foemral*. A pinna with three reniform indusia with lacerated margins. F. Elongate sorus of *Blechnum occidentale*. G. Elongate indusium of *Lomaria spicant*. G. sori of *Adiantum* H. Sori with unilateral indusia in *Asplenium lanceolatum*.

The sori in *Mattoniaceae* are ventral in position and are usually arranged in two rows on either side of the mid-rib. Each sorus ha 6—9 sporangia arranged around the receptacle. The tissue of the rece ptacle grows and overarches to form an umbrella-like indusium. Th indusial stack is trick and massive. In *Dipteridaceae* the sori are naked

In *Cyatheaceae* the ventral sori are arranged on either side of the mid-rib of pinnae and the indusium may be absent (*Alsophila*) or scale-like (*Hemitelia*) or well developed (*Cyathea*). In *Cyathea medullaris* the young sporangia are covered by hair-like outgrowths that are multicellular. In this species the indusium grows slowly. In *Hemitelia* a scale-like indusial flap develops along one side of the placenta.

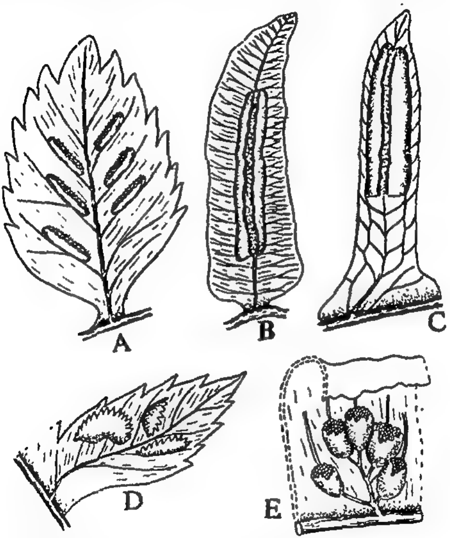

Fig. 8-8. (A—E). Fern Sori.

A. Sori with unilateral indusia in *Asplenium* lanceolatum. Sori are elongated and curved. B. *Blechnum occidentale*. Elongate sorus protected with an elongated and curved indusium. C. *Lomaria spicant*. Elongated and curved indusium. D. *Athyrium filix-foemina* A pinna with three reniform indusia with lacerated margins. E. *Matteuccia struthiopteris*. Portion of a pinna showing cup-shaped indusia with dentate margins.

(A, E, after Luerssen; B, after Diels; C, after Bower, D, Mettenius)

The sori in the Polypodiaceae are marginal in origin except for

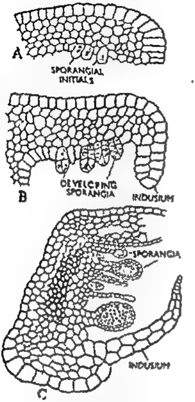

Fig. 8.9. Mixed sori in *Pteris*.
A—B. V.S. young sori of *Pteris serrulata*.
A. Showing sporangial initials arising from the ventral surface of leaf.
B. Early stages of sporangial development.
C. V.S. mature sorus of *Pteris cretica* showing indusium, placenta and sporangia.
(After Bower)

become confluent and appear as a single continuous sorus (*Pteris*). The form and development of the indusium is variable in the various sub-families of the polypodiaceae The sori are usually covered by two laterally developed indusial flaps, *e.g.*, *Pteridium* (Bower, 1918). Both these flaps originate from the receptacle (true indisium) as in *Dryopteris*. In *Pteris* and *Adiantum* (Fig. 7·8, B) the sori are protected by the inwardly turned margins of the leaflets. Such a protective device is called **false indusium**. The indusium is reniform in *Dryopteris* (Fig. 8.7, C); circular in *Polystichum lobatum* (Fig. 8.7, D); funnel shaped in *Davallia*; elongated and curved in *Asplenium lanceolatum* (Fig. 8 8, A), *Lomaria spicant* (Fig. 8.8, C) and *Blechnum occidentale* (Fig. 8.9, C). In the last named genera the sori become confluent and are covered by a common indusium. In *Lomaria* the lamina is greatly reduced. In *Athyrium filix-foemina* the indusium is reniform with lacerated margins (Fig. 8 8, D). In *Matteuccia struthiopteris*, the indusium is cup-shaped with dentate margins (Fig. 8 8, E) and is thin and papery. In this case the leaflet margins become strongly inrolled and afford additional protection to the sori. The same is the case in *Onoclea*. In *Adiantum* the sporangia develop on the underside of special marginal flaps of lamina that become reflexed (Fig. 8·7, B) and protect the sorus.

In marsileales and the salviniales the sporangia develop in sori that are borne within distinct structures called the sporocarps. The sporocarps in *Marsilea* enclose sori that contain both micro and megasporangia. In Salviniales the smaller sporocarps contain many microsporangia each and the larger ones contain one or more megasporangia per sporocarp.

According to the mode of development of sporangia in a sorus,

Bower (1935) classified the sori in ferns, into the following three types:

1. **The simple sorus.** The sporangia in such a sorus develop simultaneously and all of them mature together, *e.g.*, *Ophioglossum* and *Osmunda*.

2. **The Gradate or Basipetal Sorus.** The placentae or the receptacles are long and almost cylindrical. They bear mature or older sporangia at their distal ends and younger sporangia near the proximal or basal part. Such a sorus is found in *Dicksonia*, *Loxosoma*, *Trichomanes*, *Cyathea*, *Alsophila*, etc

3 **The Mixed sorus** (Fig 8·9). Such a sorus is an aggregation of old and young sporangia that occur mixed and show no regular arrangement in a sorus. There is no regular order or sequence of [illegible] to their age. The young and [illegible] mixed. The sporangia usually [illegible] The number of spores varies between 12—64. Such a sorus is found in majority of the living ferns, *e.g.*, polipodiaceae (*Adiantum*, *Pteris*, *Pteridium*, *Davallia*, etc.)

[illegible]

The sporangia with massive and short stalks; many layered [illegible]

[illegible]

sporangial wall, the rest of the jacket develops from the surrounding adjacent cells. The inner cell alone gives rise to the sporogenous tissue. The entire wall of the sporangium is, therefore, not derived from a single cell but from a group of cells. Such a development where the sporangium de [illegible] rangiate development.

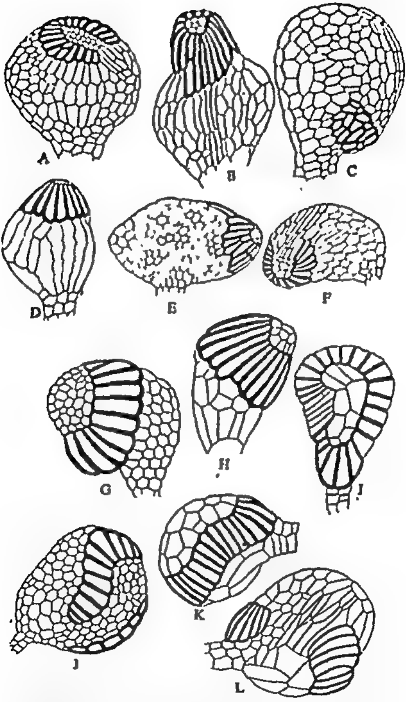

Fig. 8.10 Various types of sporangia in ferns. A. Sporangium of *Mohria cafforum*. B. Sporangium of *Schizaea dichotoma*. C. Sporangium of *Osmunda cinnamomea*. D. Sporangium of *Actinostachys oligostachys* with terminal annulus. E. Sporangium of *Lygodium reticulatum*. F. Sporangium of *Anemia phyllitidis*. G. *Gleichenia candata*, H. *Gleichenia brackniridgi*. I. *Cyathea capensis* J. *Matonia pectinata*. K—L. *Hymenophyllum dilatatum*.

rangiate feature). The innermost wall layer functions as **tapetum,** which later forms a nourishing plasr
occur in the wall, perhaps due to
and massive and develops from the
gial head or capsule and is not derived from sporangial initial or its derivatives. The spore output is large. In the Ophioglossales the sporangia produce more than 2,000 spores in *Botrychium* and up to 15,000 spores in *Ophioglossum vulgatum*. In Marattiales it varies from 1,440 in *Angiopteris*, 2,500 in *Marattia* to 7,000 in *Christensenia*.

The sp
and leptospo
tics are: (
mature spor
ous cells in
shape of sporangial
the tapetum origi-
presence of a thin

deep (Fig. 8.10)

In G[illegible] capsule (Fig. 8 10, G—H). The spore output is 128—1,024. The dehiscence is vertical.

[illegible] ial cells differentiate,

We shall now consider the **leptosporangiate type** of sporangium (Fig. 8.11, A—H). These sporangia are characterised by the following features :

1. The sporangium originates from a single superficial sporangial initial (Fig. 8 11, A), which divides into two (Fig. 8 11, B) by a transverse or oblique transverse wall. The lower or basal cell takes no further part in sporangial development.

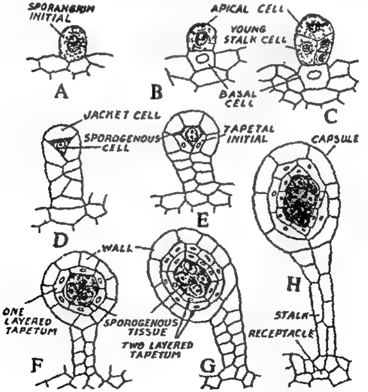

Fig. 8·11. (A—H). Various stages in the development of leptosporangiate sporangium in *Polypodium*.

2. The outer cell alone gives rise to the entire sporangium (stalk, jacket, tapetum and sporongenous tissue). The outer cell

functions as a tetrahedral apical cell (Fig. 8.10, C) which cuts off segments along its three sides. The lower segments give rise to the stalk that consists of three rows of cells. The upper three segments give rise to a portion of the sporangial wall.

3. The apical cell stops growing by the appearance of a periclinal curved wall that separates an outer jacket initial or cap cell. Now four jacket initials surround a single central cell or the **primary sporogenous cell** (Fig. 8.11, D).

4. The jacket cells divide anticlinally and give rise to a single layered sporangial wall (Fig. 8.11, E).

5. The primary sporogenous cell cuts off 4 tapetal initials (Fig 8.11, E, F) which divide both periclinally and anticlinally to form a two layered tapetum.

6. The sporogenous cell later divides to form 8—32 spore mother cells (Fig. 8 11, G, H) which undergo reduction division to produce 32—128 spores

7. The sporangial stalk is long and thin (Fig. 8·11, H).

[illegible] epistomium [illegible] **stomium**.

9. The stomium or the lip is made up of a group of 4 transversely elongated and parenchymatous cells. It is capped above by [illegible] epistomium and below by two [illegible] hypostomium The **hypostomium** [illegible] three [illegible] stalk [illegible] and [illegible]

Bierhorst (1971) considers that the terms **eusporangium** and **leptosporangium** are vague and inconsistent and should be discarded. The two types have been variously defined. D. H. campbell (1928) defined the eusporangiate sporangium as the type in which [illegible] a group of hypodermal cells generally [illegible] hesporial cell, whereas the cell out[illegible] ides to form a many layered wall and [illegible] not definite. On the other hand the leptosporangium can on the whole be traelable to a single epidermal or superficial cell and it develops as a result of a regular sequence of divisions before establishing an archesporial cell. Bower (1923) stated that a eusporangium arises from a group of cells, whereas the leptosporangium arises from a single cell and that the former is

massive and the latter is delicate. Campbell and Bower have also described int ... dilu-
tion in the di ... uspo-
rangium as ... that
divide pericli ... rma-
tion and inner cells that give rise ...
Eames defined the leptosporangium ...
of the initial, the outer cell become ...
cuts off basal cells to form a stalk unt ...
division limits growth in length. There is thus formed a central cell, usually tetrahedral in form, surrounded by a one layered wall. Anticlinal divisions in the wall divide this layer into many cells. The central cell represents the primary sporogenous tissue. From it are cut off by periclinal divisions one or two layers of thin cells which become tapetum." Such a development is considered as characteristic of the **Filicales**. The *Osmundaceaeous* sporangia are in part leptosporangiate and in part eusporangiate and are thus intermediate.

Studies in sporangial development in various pteridophytes suggest that these two types are not consistent and various grades of differences met with in each type lead to their apparent mergence. Bower described eusporangiate development in the lycopods and later in Ophioglossales and Marattiales and found many differences ... rly in many leptosporan-
... walls that are traceable
... er. Such instances have
... terms eusporangiate and
leptosporangiate obsolete.

Further Bierhorst (1971) regards that the ancestral filicalean sporangium must be an elnogated structure situated at the tip of an aerial axis and lacks annulus and dehisces longitudinally. Such a sporangium has been r ... *phyton*
(Trimerophytaceae) which ... *ferns*
and fern-like plants. It ... oran-
gium developed from a single initial which was also the apical cell of the axis. The development was leptosporangiate as the initial produced lateral segments and then stopped producing them after dividing by a dense-shaped periclinal wall (leptosporangiate character). The outer cell produced outer wall layer and the inner one produced tapetal layers, sporogenous tissue and some inner wall layers. Such a discovery contradicts the previously held view that eusporangium and massive sporangia are primitive. *It indicates* that leptosporangium is primitive.

... the pioneer structures of the gameto-

layers. In the primitive ferns like Ophioglossales, the plasmodial fluid is consumed by the developing spores. In some of the advanced

ferns the plasmodial fluid remains as a deposit on the outermost wall of the spore. This deposited plasmodial fluid is often designated as the **"perispore"** or **perine.** The perispore is present in Asplenieae and Aspidieae. In the megaspore of *Salvinia* the perispore forms a characteristic layer with pollen-chamber like depression at its apex. The spores may be tetrahedral in shape or bilateral with two flattened sides. At the **proximal end** of the spore, there is a tri-radiate or a monolete aperture, a portion where the exine is fissured. The spores are usually shed after separation from the tetrad, *i.e.*, they are liberated in a one celled condition. In *Christiopteris tricuspis* the spores are shed two or three together (Nayar, 1967). Mostly the spores remain dormant for a variable period after shedding, but in *Osmundaceae* they have little dormant period and germi-
... and *Vittaria*.
... The period
... remain viable
for a few days; whereas in *Onychium* they remain viable for over a year. The spore has usually a centrally placed nucleus surrounded by vacuolate cytoplasm that has chloroplastids or leucoplastids and oil globules suspended in it. Majority of ferns are homosporous but *Marsileales* and *Salviniales* are heterosporus. The plasmodial fliud in the sporangia of *Azolla* forms charactristic structures called the massulae.

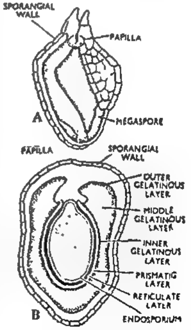

Fig. 8 12. Mature megasporangia of *M. diffusa* containing fully mature megaspore. (After Boteborg)

Regarding polarity of the spore, it has **proximal pole** (the end directed towards the centre of the tetrad) and a **distal pole** (end directed towards outside). The hypothetical line connecting the two poles is called **polar axis,** and the one perpendicular to it is the **equatorial axis.** If the equatorial axis divides the spore into two equal polar faces, the spore is isopolar, otherwise it to heteropolar.

The spore wall encloses the spore protoplasm and usually consists of two layers : **exine** and **intine.** Intine is colourless. The exine or the outer covering is further made up of two layers :—

(*i*) the outer layer as the **ectine** (*Syn-Sexine* of Erdtman, 1952) ; and (*ii*) the inner layer or **endine** (Syn-Nesine of Erdtman, 1952). The ectine is made up of elongated or columnar and radially placed rods called the **columellae.** The columellae may be free at their tips or may be united to form a continous layer called **tegillum or tectum.** Perine, as stated above, may be

absent. It is usually absent in trilete spores (except in *Adiantum* and *Cheilanthes*), and may be present or absent in monolete spores.

The **ectine** or the outer layer of exine is variously ornamented. The ornamentation is due to the arrangement of **columellae** or due to some outgrowths on the ectine. These ornamentation patterns are considered to be of great taxonomic importance. In case the columellae are free at their ends the pattern is called **pilate**. In many pteridophytes the free ends of columellae are fused and the columellae are arranged in distinct patterns, *e.g.*, **reticulate** when they form a network (*Schizaea laevigata* and some *Osmundaceae*), **striate** when they are parallel (*e.g.*, *Schizaea*); **rugulate** when they anastomose (*e.g.*, *Cheilanthes farinosa*). In many cases the upper ends of columellae are fused to form a layer called the **tegillum** or **tectum** and this layer bear many types of outgrowths or excrescences which are usually of following types:—

(*i*) **Granulose** when they form a granular or grain-like pattern, *e.g.*, *Tmesipteris*, *Mohria*, *Schizaea bifida*, etc.

(*ii*) **Spinulose** when outgrowth, are spine-like with pointed or blunt end, *e.g.*, *Psilotum*, *Selaginella fruticulosa*, etc.

(*iii*) **Verrucate** when there are wart-like unconstricted outgrowths, *e.g.*, *Pyrossia beddomiana*, *Selaginella mongolica*, etc.

(*iv*) Tuberculate when in the form of finger-like tubercles, *e.g.*, *Osmunda* and *Todea*.

(*v*) **Baculate** when the outgrowths are rod-shaped, *e.g.*, *Selaginella haematodes*.

(*vi*) **Saccate** when vesicular outgrowths arise, *e.g.*, *Selaginella parkei*, *S. rupestris*, etc.

(*vii*) **Psilate** when there are fine dots on the surface, *e.g.*, *Cheilanthes chrysophila*, *Loxogramma involuta*, *Pyrossia fissa*.

Recently (Machlis and Rawtischer-Kunkel, 1967) very interesting observations have been made on the megaspore of *Marsilea vestita*. These authors studied the structure of dry megaspore as well as of megaspores immersed in water. The dry megaspore (Fig. 8·12) of this species, while it is still enclosed within the megasporangium, is surrounded by an acellular mass formed by the tapetum (which is two to three cell layers thick) and the aborted megaspores. This acellular mass differentiates into a number of layers. The megaspore has an almost oval shape with a small papilla at its apex. Both the megaspore protoplast and the papilla are completely surrounded by the endospore. Boterburg (1956) reported that the endospore or intine is further differentiated into two layers. Next to the endospore is the exine or exospore which is composed of five layers. These are from within outwards: (*i*) reticulated layer; (*ii*) prismatic layer; (*iii*) inner gelatinous layer; (*iv*) middle gelatinous layer; and (*v*) outer gelatinous layer. Boterberg

(1936) has also reported the same constitution of the megaspore wall in *Marsilea diffusa*.

On immersion in water the layers of exine or exospore absorb water and expand to form a gelatinous mass that can be differentiated into following parts:

(*a*) **The papillar envelope** (Fig. 8·13). The exine in the apical and papillar region of the megaspore swells to form a gelatinous mass that is thrown into longitudinal ridges. This is called the **papillar envelope** because it surrounds the papilla of the megaspore. Later this papilla develops into a single and reduced archegonium. The papillar envelope is tough in consistency.

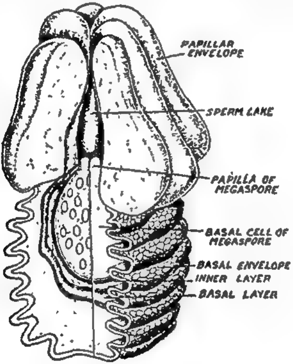

Fig. 8·13. Hydrated megaspore of *M. vestita*.
(For explanation see text)
(After Machlis and Rawtischer)

(*b*) **The basal envelope** (Fig. 8.13). The lower larger portion of the megaspore is surrounded by the gelatinised exine that shows horizontal folds. This is called **basal envelope** and is of softer consistency.

(*c*) **Funnel** (Fig. 8·14). Within the papillar envelope, there is thick-walled bell-shaped structure called **bell** (Fig. 8·14). The bell encloses a liquid interior which is termed as **sperm lake** (Fig. 8·14). The bell and the sperm lake together constitute a structure [illegible] funnel [illegible]
apical [illegible]
after [illegible]

(*d*) **Basal Layer** (Fig. 8.14). It completely surrounds the lower portion of the hydrated megaspore and extends towards the base from the bell. Basal layer appears to be a separate layer as it separates *from* the bell after some more exposure to water. In does not cover the papilla.

(*e*) **Inner layer.** *It is* completely enclosed by the basal layer and lower part of the bell (Fig. 8·14).

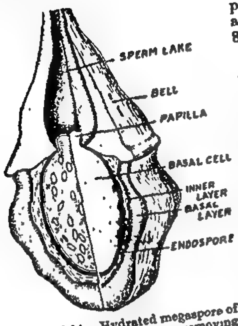

Fig. 8·14. Hydrated megaspore of *M. vestita* as seen *after* removing the papilla and basal envelope. (After Machlis and Rawtscher)

Next to the inner layer is the intine which encloses the entire megaspore along with *its* apical papilla. It ruptures in the papilla region, *only* after the papilla develops into an archegonium.

In the megasporangium of *Azolla* the disorganised tapetal layer forms *four* alveolar structures called the massulae. One of these massulae surrounds the functional megaspore. The other three massulae contain the nonfunctional *megaspores*. The mature functional megaspore is liberated by the transverse dehiscence of the megasporangial wall and the indusium. The upper parts of the indusium, megasporangial wall and the three massulae containing non-functional spores remain attached to the upper end of the massula enclosing the functional megaspore. They form the so-called "swimming apparatus" of the megaspore.

Similarly massulae *are* formed around the microspores but in this the massulae bear numerous pin like *processes* called the **glochidia.** The glochidia help in attaching the massulae *containing* the microspores to the massula enveloping the megaspore. The microsporangiate massulae *enclose* large number of spores, each. The massulae *originate* from the abortive *mother* cells and the tapetal plasmodium and are regarded as specialised perispore. In the microsporangium of *Azolla* 64 microspores are formed. They migrate towards *the* periphery of the sporangium and get embedded in peripheral plasmodial layer formed by the *disorganisation* of tapetum. A number *of* vacuoles appear *in* the plasmodium. Groups of miscrospores get embedded *in* these vacuoles. Each vacuole later becomes partitioned by the appearance *of* irregular septa, giving it an alveolar appearance. This alveolar structure, called the **massula,** encloses a group of microspores. The glochidia appear as finger-like processes from the wall of the massula. Each such process becomes barbed at the apex.

Prothallus or the Gametophyte

Spore is the pioneer structure of the gametophyte and germinates to give rise to the prothallus whose function is to bear the sex organs. The germination of the spore follows a different course in the homosporous and the heterosporous ferns. The spores in the homosporous ferns form **exosporic gametophytes.**

Early Stages of Germination

The conditions necessary for the germination of the spore are :

(*i*) suitable moisture ; (*ii*) adequate temperature ; (*iii*) pH range 4—8 ; and (*iv*) sufficient light intensity of suitabe quality.

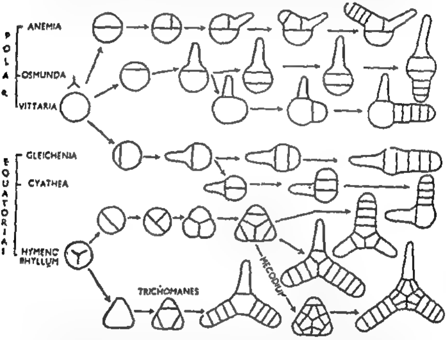

Fig. 8 15. Earlier stages of spore germination in homosporous ferns. The proximal pole of the spore is indicated by the tri-radiate mark.

(After Nayar and Kaur, 1971)

crease

mark.

the Homosporous ferns, the patterns of spore germination have been variously classified. Momose (1942) recognised three types of spore germination : (*i*) **Centripetal** in which the rhizoid is ...

basal cell of the thallus and is pe

in which the thallus grows in

primary rhizoid ; (*iii*) **Tangenti**

at the region of the cross wall b

next to it. Nishida (1965) renan

types as the **Polypodioid** and **Aspidioid** types, respectively and

added another type called the **Tripolar-type** to accommodate the Hymenophyllaceous germination in which a tripolar plate is formed. Nayar and Kaur (1968, 1971) regard these classifications as *incorrect because they do not take into consideration the polarity of* the germinating spore. They have proposed their own classification based on planes of cell division and polarity of spore (Fig. 8·15). They recognised three distinct categories :—

1. **Polar Germination** (Fig. 8·15). In this type of germination the first wall of the spores is parallel to its equatorial plane. The growth and elongation of primary rhizoid and the young thallus is parallel to the *polar axis of the spore.* This type is further sub-divided into three sub-types :—

(*a*) **Osmunda type.** It is found in *Osmundaceae* and is the simplest type of polar germination. The first wall cuts off a small *primary rhizoidal initial* that grows parallel to the polar axis, into a primary rhizoid. The other cell divides by one or two or even more walls parallel to the first wall *(Fig. 8·15) into a short uniseriate germ filament.* The germ filament and the rhizoid grow in opposite directions.

(*b*) **Anemia type** (Fig. 8·15). In this type the spore divides into two equal cells of which the distal one remains inactive *throughout. The proximal cell divides by wall perpendicular to* the first to cut off a small lateral **rhizoid initial** and a large **prothallial initial.** The prothallial initial divides by a series of walls parallel to the first wall and grows into a germ fila*ment that elongates in a direction parallel to the polar axis of* the spore (facing the proximal pole). The primary rhizoids elongates parallel to the equatorial axis of the spore. This type is characteristic of *Anemiaceae* and *Lygodiaceae* of Nayar.

(*c*) **Vittaria type** (Fig. 8·15). It is the commonest type of polar germination. The first division is similar to Osmunda type. The smaller cell grows into a primary rhizoid that elongates parallel to the polar axis. The larger or the distal cell acts as the prothallial initial and divides by a wall perpendicular to the first wall into two equal daughter cells. One of them remains inactive and the other divides by series of walls parallel to the second wall into a germ filament that is perpendicular to the primary rhizoid

2. **Equatorial Germination.** In this type of germination (Fig. 8·15) the first wall of the spore is formed parallel to the polar axis of spore. The prothallus elongates in a plane parallel to the equtorial plane of the spore. It is further sub-divided into six types :—

(*a*) **Gleichenia type** (Fig 8·15). It is characteristic of *Gleicheniaceae, Dipteridaceae, Loxogrammaceae* and most of the *Polypodiaceae.* The first wall is *parallel* to the polar axis *cutting off a* small primary rhizoidal and a large prothallial cell. The primary rhizoidal cell elongates into a laterally placed rhizoid, whereas the

prothallial cell divides by a series of walls parallel to the first wall forming a germ filament. Both the primary rhizoid and the germ filament elongate along the equatorial plane of the spore in opposite directions.

(*b*) **Christiopteris type.** It is a variation of the above type. In this case the germ filament develops as in the above case, but usually it remains short or may even end in a rhizoid. Secondary germ filaments develop as branches from any one or more cells of the primary filament; the branches are perpendicular to the primary filament.

(*c*) **Cyathea type** (Fig. 8·15). It is found in *Cyatheaceae*, *Loxsomaceae* and *Cheiropleuriaceae*. The rhizoid initial develops as in Gleichenia type, but the second division in the prothallial cell is perpendicular to the first division and the subsequent divisions are parallel (Fig 8.15), so that the rhizoid grows perpendicular to the germ filament or along the equatorial plane of the spore and the germ filament grows along the polar axis of the spore.

(*d*) **Hymenophyllum type** (Fig 8·15). In this case the first two walls are perpendicular to each other and divide the spore into "an equatorially expanded plate" of three equal cells. Each of these three cells divides by a peripheral wall to cut off three lens-shaped cells. One of these lens-shaped cells may grow into a primary rhizoid and the remaining two into two germ filaments, or two of the lens-shaped cells may grow into rhizoids and one into a germ filament. During the formation of a germ filament further divisions are parallel to the last formed wall.

(*e*) **Trichomanes type** (Fig. 8.15). In this case the first two divisions of Hymenophyllum type are omitted with the result that three lens-shaped cells are formed simultaneously at the periphery of the triangular spore. Further development is like the Hymenophyllaceous type.

(*f*) **Mecodium type** (*Fig.* 8·15). *It is like the* Hymenophyllaceous type up to the formation of three cells. Extra divisions occur in these three cells resulting in the formation of a [illegible] to 12 celled triangular plate of cells, one cell in thickness. It is expanded along the equatorial plane of the germinating spore. Three lens-shaped peripheral cells are cut off in this plate, at each corner, and develop further as in the Hymenophyllaceous type.

3. **Amorphous Germination.** It is characteristic of some primitive ferns, *e.g.*, *Marattiaceae*, *Matoniaceae*, *Ophioglossaceae*, a few members of *Schizaeaceae* (*Actinostachys* and *Lophidium*) and *Gleicheniaceae* (*Stromatopteris*). The spore divides without any polarity in cell divisions and direction of growth. It results in a plate of cells in which a meristematic cell is differentiated in one of the peripheral marginal cells. Further growth of the prothallus is in the direction of the meristematic cell.

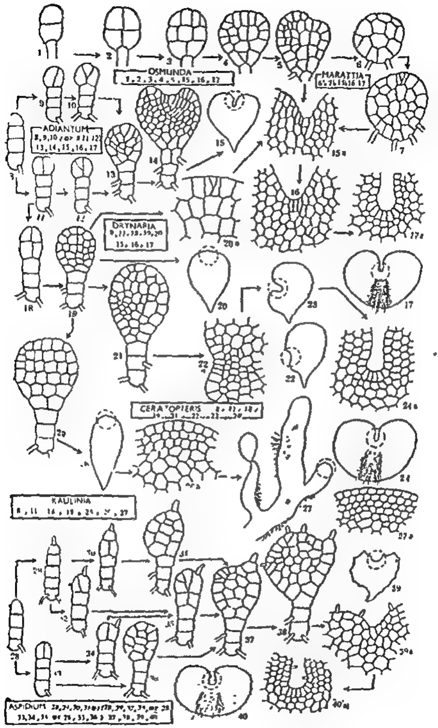

Fig. 8·16. Later stages in spore germination in homosporous ferns. (After Nayar and Kaur, 1971). The various types are indicated by numbers. Each specified type with regard to its numbers is given within squares and rectangles.

Later Sages of Development (Fig. 8·16). These stages lead to the development of a characteristic adult prothallus or the gametophyte. Nayar and Kaur (1969, 1971) recognised seven different patterns among the homosporous ferns. These are briefly described below :—

1. **Osmunda Type** (Fig. 8·16). It is characteristic of *Osmundaceae* [illegible] ent turns into a plate of 4 cells by [illegible] ell. In case the germ filament is [illegible] of cells will divide to form 4 cells. [illegible] form a circular plate of prothallial cells. A meristematic cell is established in a marginal cell. The quadrant in which the meristematic cell appears grows more and the prothallus assumes an asymmetrical shape (Fig. 8·16). The young thallus elongates and later becomes notched at the growing region. It later on assumes a symmetrical cordate shape as in Adiantum type.

2. **Marattia Type** (Fig. 8·16). In this case spore germination is of amorphous type resulting a circular plate of cells that may later become two or more cells thick. A meristematic cell is established, notch appears and ultimately a cordate prothallus develops. Later growth is like the Adiantum type.

3. **Adiantum Type** (Fig. 8·16). In this case the terminal cell of the germ filament divides first by an oblique wall followed by a wall perpendicular to it. This establishes a meristematic cell flanked an either side by two cells Sometimes the terminal cell of the fiament divides by a wall parallel to the long axis of the filament followed by a second oblique wall cutting of a median cell, which in turn divides by a wall perpendicular to the second oblique wall. This cuts off a median meristematic cell. The meristematic cell divides by walls parallel to the oblique wall, each wall being perpendicular to the one preceding it. These divisions and further divisions of the daughter cells lead to the formation of an obovate plate of cells which later becomes notched in the region of the meristematic cell (Fig. 8·16). The meristematic cell then divides by a transverse wall (Fig. 8·16). The anterior daughter cell divides by two or three walls parallel to each other but perpendicular to the original transverse wall, forming a row of two or three cells. These cells are elongated in the direction parallel to the long axis of the thallus and constitute the 3-celled meristem. These cells divide by walls parallel either to their lateral or basal walls. These divisions in two planes lead to the formation of a mid-rib behind the meristematic region in the median plane of the prothallus and a cordate prothallus with semicircular lateral wings.

4. **Drynaria Type** (Fig. 8·16) In this type the formation of apical cell (meristematic cell) is delayed, and the terminal cell of the germ filament divides by longitudinal and transverse walls into a spathulate plate of cells (Fig. 8·16). At a later stage the meristematic cell is distinguished in one of the marginal cells of this plate,

by two oblique divisions (Fig. 8·16). Later divisions are exactly similar to the Adiantum type and lead to a cordate prothallus with a terminal notch.

5. **Kaulinia Type** (Fig. 8·16). It is like *Drynaria* type upto the formation of a spathulate plate. In this case no meristematic cell is formed. All the cells of the prothallus divide actively. The prothallus elongates and becomes ribbon-like with rounded anterior ends (Fig 8·16). Branches may arise from the marginal cells. There is no midrib At maturity irregular cushions of two to four cells in thickness may develop along the median plane of the prothallus.

6. **Ceratopteris Type** (Fig. 8·16). It is also similar to *Drynaria* type up to the formation of a spathulate plate of cells. Now in some cases the anterior cells of the germ plate may not grow further or grow very slow and take no further part in the development of the prothallus. The inter calary cells, instead, divide actively and gradually the meristematic activity becomes restricted only to some marginal cells on one side and away from the apical portion (Fig. 8·16). Later a lateral notch appears. The meristematic cells lie at the base of this notch, which goes on becoming pronounced. Later a mid-rib develops behind the meristematic region. The young prothallus is cordate but asymmetrical with one wing larger than the other or in extreme cases only one wing is developed. In some cases the marginal meristem becomes apical by unilateral growth of both the wings, thus making the prothallus cordate.

7. **Aspidium Type** (Fig. 8·16). It shows great variations in development. These variations are conditioned by the development of a hair. Usually the terminal cell of the germ filament grows into (Fig. 8·16) a unicellular hair. This cell becomes sluggish and takes no part in prothallus development. Sometimes a few cells below the terminal cell also remain sluggish and the posterior cells of the filament divide actively to form a plate of cells (*Fig.* 8·16). This plate is lopsided i.e., one side is broader than the other. The larger side of the plate [illegible] meristematic cell by two oblique divisions of one [illegible] some cases the terminal cell [illegible] inally into a smaller cell and a [illegible] hair. The smaller cell divides actively and produces the prothallial plate (Fig. 8·16). The plate is slightly lop-sided at its anterior end. A meristematic cell appears in the margin. Marginal unicellular hair always develop from the prothallial plate. In another variation hair development is delayed until the terminal cell of the filament has divided longitudinally. One of the two cells grows slowly and divides, ultimately bearing of hair. The other cell divides actively to form a plate which develops a marginal meristematic cell. *Later* development is like the Adiantum type (Fig. 8·16).

All these variations described above may occur in the same species. The young thalli are asymmetrical, cordate and lopsided

due to marginal meristematic cell being lateral. Later growth, no doubt, results in the loss of asymmetry and finally a symmetrical, cordate prothallus is produced (Fig. 8 16). Marginal hair are profuse, so are the superficial ones,

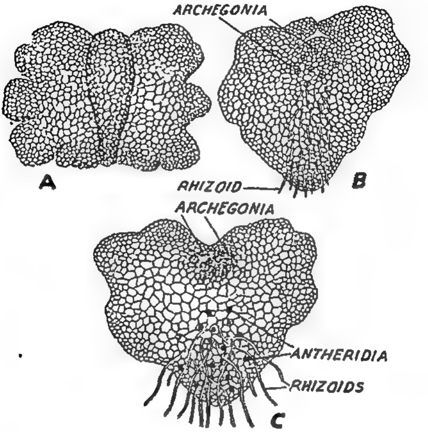

Fig. 8 17. (A—C). Cordate prothalli of filicophyta. A. Prothallus of *Gleichenia*, B. Prothallus of *Cyathea*; (C) Prothallus of *Nephrolepis*

The net result of spore germination is the prothallus that also varies in shape, size and structure. Cases are not rare where the prothallus in the same genus or even in the same species shows variations in form and size (*Dryopteris*, *Schizaea*, etc.).

The Adult Prothallus

Bower (1923, 1935) recognised three types of prothalli in the ferns. These are :—

(*i*) The cordate type or heart-shaped prothallus. (*ii*) The filamentous type. (*iii*) The mycorrhizic type.

Nayar and Kaur (1971) recognised 5 types of adult prothalli in the homosporous ferns. These are ; (*i*) **cordate** ; (*ii*) **filamen-**

tous ; (*iii*) **strap shaped** ; (*iv*) **ribbon-shaped** ; and (*v*) **tuberous.** These are described below.

The Cordate Type. It is the most common type of prothallus (Fig. 8 17 A—C) found among th [illegible] *lepis*, *Pteridium*, *Pteris*, *Adiantu* [illegible] *ceae*, *Dipteridaceae*, *Matoniaceae*, *Osmundaceae*, *Marattiace* and *Cyatheaceae* In the *Polypodiaceae* the spore gives rise to a short filament of 3 to 6 cells. The terminal cell of this filament divides by two oblique vertical walls that cut off an apical cell The activity of this apical cell leads to this formation of a green plate of cells with an apical notch. Later the apical cell is replaced by a row of meristematic cells. Under suitable conditions of growth and nourishment this notched plate develops into a heart-shaped or a cordate prothallus. The gametophyte is one cell in thickness except in the region posterior to the notch, where it is many celled thick. The sex organs and rhizoids develop on the ventral side. Under crowed and undernourished conditions the prothallus becomes filamentous, *e g.*, *Dryopteris* and bears only antheridia. It can develop into a more or less cordate type if transferred to suitable environmental conditions. Normally the prothallus is **monoecious.** The prothallus in *cyatheaceae* also r [illegible] its shape and structure, but di [illegible] ment. In this case the short filam [illegible] to form a plate of green cells [illegible] the beginning). The apical cell [illegible] cells. Later it is replaced by [illegible] development is similar to that of polypodiaceous prothallus. In *Cyathea* the prothalli bear distinct scale like hair on its surface. In Dipteridaceae (*Dipteris conjugata*) the spore germinates to form a plate of cells which later develops into a cordate prothallus with sinuate or ruffled margins. The sex organs usually develop on the ventral surface but they can also develop on the dorsal side. The spores in *Osmunda* are green and, therefore, germinate immediately after their release. The germ tube divides transversely into a lower **rhizoidal cell** and an upper longer **prothallial cell.** The latter develops into a filament of few cells. The terminal cell divides to cut off a two-sided apical cell whose activity leads to the formation of a cordate prothallus Later the two-sided apical cell is replaced by a 4-sided apical cell or a group of two or three *initials.* They divide to cut off segments dorsally as well as ventrally and laterally to form a mature cordate prothallus traversed by a distinct midrib.

The cordate prothalli in *Anogramme* bear storage tubers that grow into the soil and serve as perennating organs.

The Filamentous Type [illegible] prothallus is charac [illegible] of the family [illegible] prothalli have, no doubt, been seen to develop in several ferns but they are the result of abnormal environmental conditions. In *Schizaea* and

Trichomanes filamentous condition persists under all circumstances. The prothalli in both these genera resemble some branched algal

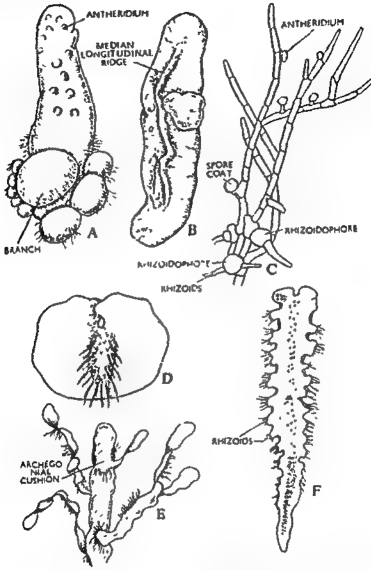

Fig. 8·18. Mature prothallus types of homosporous ferns.
A. Tuberous prothallus of *Helminthostachys*. B. Tuberous prothallus of *Botrychium*. C. Filamentous prothallus of *Schizaea pusilla*. D. Cordate prothallus of *Adiantum caudatum*. E. Ribbon shaped prothallus of *Paraleptochilus decurrens* (Polypodiaceae). F. Strap-shaped prothallus of *Elaphoglossum* sp.

filaments or moss protonemata. Some of the branches penetrate the soil and act as rhizoidal branches, whereas others are green and transversely septate. In *Schizaea pusilla* (Britton and Taylor, 1901) the rhizoids are unicellular and develop from specialised short branches whose cells are infected with a mycorrhizic fungus. The sex organs

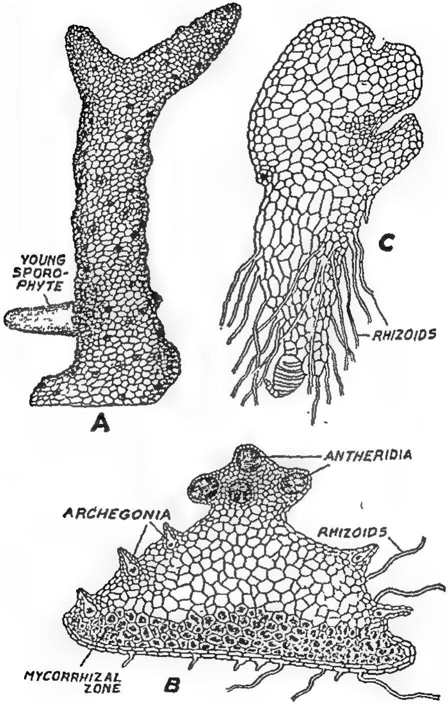

Fig. 8·19. Prothalli of filicophyta,
A. Underground and mycorrhizic prothallus of *Ophioglossum*.
B. Section through the mycorrhizic prothallus of *Botrychium*. Note the mycorrhizic portion and position of sex organs.
C. Cordate prothallus of *Ceratopteris*.
(A, B after Haupt; C after Smith)

are seated on unicellular lateral branches. In *Trichomanes* the antheridia occur on any branch of the filamentous prothallus but archegonia appear in clusters (Fig. 8·18, B) on specialised multicellular structures called the archegoniophores.

Strap-shaped Thallus. This is found in the family Grammitidaceae and some Lomariopsidaceae and Polypodiaceae. In *Rhipidopteris peltata* and *Elaphoglossum stenophyllum* the thalli are long and strap-like with fimbriated and hairy margins. The breadth of the thallus is intermediate between cordate type and ribbon-shaped prothalli. They are much longer than broad (Fig. 8.18, F) and are slow growing and unbranched with cordate apex. The apical meristem is pluricellular, the midrib is thin and interrupted. Sex organs and rhizoids are borne on the midrib. The rhizoids may occur along the margins too.

Ribbon-shaped Thallus (Fig. 8.18, E). It is found in *Loxogrammaceae, Vittariaceae and some Hymenophyllaceae and Polypodiaceae.* The thalli are thin, one cell in thickness, flat, dorsiventral, perennial and slow growing. It is devoid of a mid-rib and has rounded apex that has no well defined meristem. It is usually profusely branched.

ginal clusters.

The Tuberous Type. This type of prothallus is prevalent in the Ophioglossaceae. *Helminthostachys* affords a very good example of such a type of prothallus (Fig 8 18, A). In this case the prothallus is saporophytic in nutrition and is mostly underground or subterranean. The underground portion of the prothallus is lobed and is attached to the soil by means of rhizoids It is also called the vegetative region of the prothallus. From the vegetative region arises a cylindrical branch that grows vertically upwards and bears

remain
lindrical
fungus
extend
ry slow
growing.

The mature gametophytes of *Ophioglossum* may be cylindrical Fig. 8.19, A), conical or irregular in shape. They may be branched or unbranched. They are usually wholly subterranean or in some cases partly above ground and partly underground.

In *O. pedunculosum* the exposed portion of the prothallus assumes green colour and may become flattened and irregularly lobed. The prothalli are usually perennial but Campbell (1907) reported that prothalli of *O. moluccanum* are annual. The endophytic fungus is confined to the inner cells of the older portion of the prothallus. The younger regions are free from the symbiotic fungus. In *Ophioglossum* the thallus grows by means of a 4-sided apical cell.

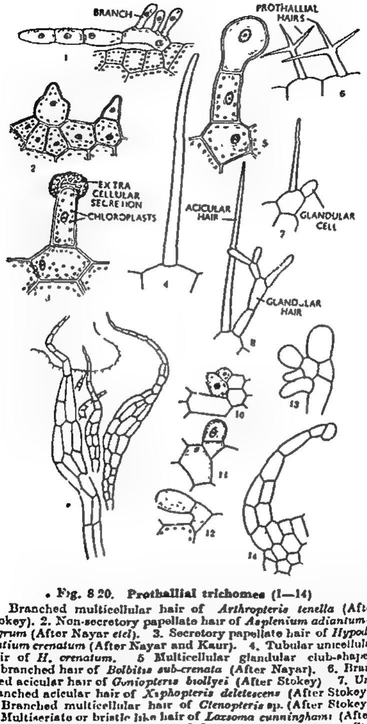

Fig. 8.20. Prothallial trichomes (1—14)

1. Branched multicellular hair of *Arthropteris tenella* (After Stokey). 2. Non-secretory papellate hair of *Asplenium adiantum-nigrum* (After Nayar *etel*). 3. Secretory papellate hair of *Hypodematium crenatum* (After Nayar and Kaur). 4. Tubular unicellular hair of *H. crenatum*. 5 Multicellular glandular club-shaped unbranched hair of *Bolbitis sub-crenata* (After Nayar). 6. Branched acicular hair of *Goniopteris biollyei* (After Stokey) 7. Unbranched acicular hair of *Xiphopteris deletescens* (After Stokey). 8. Branched multicellular hair of *Ctenopteris* sp. (After Stokey). 9. Multiseriate or bristle like hair of *Loxsoma cunninghamii* (After Stokey). 10—12. Development of Gleichenaceous hair in *Sticheurus bifidus*. It develops from a wedge shaped initial (10) which possesses chloroplasts. Later it bears a glandular apical cell. 13. Branched glandular hair of *Lepisorus normalis* (After Nayar). 14. Unbranched—multiseriate hair of *Anemia* sp. (After Atkinson).

The gametophytes of *Botrychium* (Fig. 8.10, B) are also mycorrhizic and may be cylindrical or have a tendency towards flattened and dorsiventral form (*Botrychium virginianum*). There is no well defined meristem in *Helminthostachys* and *Botrychium*.

Such prothalli are found in *Actinostachys* and *Lophidium* of Schizaeaceae, and *Stromatopteris* of Gleicheniaceae.

The Prothallial Trichomes (Fig. 8 20, 1—14). The prothalli of some homosporous ferns are beset with trichomes that can be conveniently classified into two headings which can further be sub-divided into sub-headings as below:

Trichomes

- A. Unicellular trichomes (Fig. 8)
  - Papillate 1
    - Secretory or glandular 1
    - Non-secretory or non-glandular 2
  - Acicular 2
  - Tubular 3
    - Unbranched 1
    - Branched 2
- B Multicellular trichomes (Fig. 8)
  - Multiseriate Multicellular hair (e.g., *Loxsoma cunninghami*) 1
  - Unbranched Multicellular hair (Uniseriate) 2
  - Branched Multicellular hair (Uniseriate) 3
  - Glandular or Club-shaped (Uniseriate)
    - Gleicheniaceous 1
    - Branched 2
    - Unbranched 3

The trichomes may be present all over the prothallus or may be restricted only to margins or the surface. The trichomes may appear during [illegible] etc.) or [illegible] and sor[illegible] shaped initial cells. The accompanying figures illustrate the structure and examples of these trichome types. The hair have usually vacuolated cytoplasmic contents and may possess chloroplasts. Acicular hair are devoid of contents at maturity.

Vegetative Propagation of the Prothallus. Vegetative propagation of mature prothalli of homosporous ferns is quite common. It is effected by following methods:—

1. **Regeneration by Branches.** It is very common among the ribbon like and filamentous-branched prothalli. The older portions of the prothalli degenerate setting free the younger branches, which under certain conditions develop into new prothalli. In some cases branches arising from superficial cells develop into new prothalli. This type is common among Hymenophyllaceae, Schizaeaceae, Vittariaceae and some Polypodiaceae.

2. **By the Formation of Germ Filaments.** In [illegible] *mollissima* the young prothallus produces moniliform germ [illegible]

(Fig. 8.21, A) that easily break into fragments each of which develops into a new prothallus.

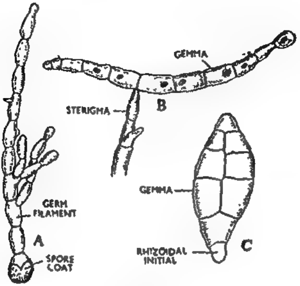

Fig. 8.21. Vegetative propagation of prothalli in homosporous ferns

A. Germ filament of *Ctenopteris mollissima* (After Stokey). B. Gemma of *Polyphlebium venosum* attached laterally to sterigma (After Stone). C. Spindle-shaped Gemma of *Mecodium* with basal rhizoid initial (After Stone).

3. **By the Formation of Gemmae** (*Fig.* 8·21, B, C). These are specialised, unicellular or multicellular structures borne on sterigmata and are capable of germinating into new prothalli. In some Polypodiaceae (*Kaulinia, Colysis, Leptochilus* and *Paraleptochilus*) the gemmae are unicellular or dumbell-shaped and densely chlorophyllous. In *Vittariaceae* and some *Hymenophyllaceae* the gemmae are multiseriate and spindle-shaped (Fig. 8.21, C) are attached by an end cell to the sterigmata. In *Trichomanes* and *Polyphlebium venosum* the multicellular and filamentous gemmae are borne perpendicular to the sterigmata (Fig. 8·21, B). Such filamentous gammae may become 10—12 cells long. Such gemmae produce germ filaments that develop into prothalli. On detachment the gemmae attach themselves to the substratum by producing rhizoids.

T[illegible] an interesting case. Thoy have lost th[illegible] vegetatively coverir[illegible] gard them as the protnallus of *Vittariaceae* that have lost the sporophytic stage by reduction and reproduces only by vegetative propagation of the prothallus.

The sex organs. The sex organs develop on the gametophyte and are always multicellular and jacketed. The male sex organs

are called **antheridia** (singular-antheridium) and the female are known as **archegonia** (singular archegonium). Both may arise on the same prothallus or they may be borne on different prothalli. In the former case the prothallus is bisexual or **monoecious**, whereas in the latter case it is unisexual or **dioecious**. Bisexual prothalli may be **protandrous** or **protogynous**. The antheridia produce male gametes or the sperms or antherozoids that are flattened structures and require a liquid medium to swim to the female sex organs containing eggs The number of sperms produced per antheridium varies considerably. It may be from more than one hundred (*Ophiglossum*) to 16 to 32 sperms per antheridium as in *Dryopteris*, *Pteris*, *Pteridium*, *Adiantum*, etc. The female gamete or the egg is nonmotile and is present in the venter of the archegonium. The archegonia show a remarkable uniformity in their structure and development and in possessing a single egg. Rarely they contain more than one egg

The hermaphrodite prothalli usually produce antheridia earlier than the archegonia. Antheridial development often begins before the differentiation of the mid-rib or even before the organisation of the plate like stage. The archegonial development starts after the formation of the mid-rib or the cushion or cushions, as the case may be. It has been noticed that unfavourable growth conditions lead to the production of male prothalli and exceptionally favourable conditions tend to produce only female prothalli, whereas less favourable conditions favour the production of bisexual prothalli. Nutritional conditions of the substratum and availability of light affect the sex of the prothallus (Sossuntzov, 1954; 1957; Hurel-Py 1950; Schraudolf, 1967). Recently it has been shown that antheridia formation in the ferns is controlled by chemical substances called the **antheridiogens**. Antheridiogens are specific for certain groups of plants, *i.e.*, an antheridiogen effective in *Pteridium* may not be effective in *Ceratopteris* and *vice versa* (Dopp, 1950, 1959; Naf, 1956, 59, 60, 65; [illegible] eridiogens are produced [illegible] diffuse into the substra- [illegible] ..ntheridial formations in species sensitive to the particular antheridiogen.

Position of the sex organs. As has been stated before, the gametophytes may be exosporic or endosporic. The former are typical of the homosporous forms whereas the latter are restricted to the heterosporous pteridophytes. The endosporic gametophytes are completely or partially enclosed by the spore wall. The exosporic gametophytes are free living and are not surrounded by the spore wall. They represent the primitive type of prothalli and are usually monoecious or may become dioecious due to certain changed environmental conditions.

The sex organs in the exosporic gametophytes may be embedded in the gametophytes tis[illegible] emergent type. The former i[illegible] whereas the latter type is [illegible]

ferns. In *Ophioglossum vulgatum* and other species of this genus the sex organs are sunken in the prothallus tissue (Fig. 8·19 A). In *Botrychium virginianum*, a member of ... are sunken, but the archegonia have ... B). The sex organs develop on the ... in *Ophioglossum*, that arise from the lo... in an acropetalous manner. The antheridia are numerous and develop in an irregular sequence all around the cylindrical body. In *Marattiaceae* (*Marattia, Angiopteris*), the dorsiventral prothallus is monoecious and bears antheridia on both the dorsal and the ventral surfaces. In *Ceratopteris* the antheridia are partially embedded in the prothallus tissue (Fig. 8·22, 12) and are borne along the margins. The archegonia are confined only to the ventral surface and occur along the central cushion along with the rhizoids. The antheridia and the archegonia are both sunken in the prothallus tissue. The sex organs in Osmundales arise on the ventral surface of the prothallus and project above the surface (emergent type). The antheridia ... argins or on the ventral side of the ... of the prothallus. The archegonia ... distinct mid-rib and have projecting necks. In some of the *Osmundaceae* young archegonia are also found mixed with older ones. Majority of the leptosporangiate ferns have their sex organs distributed on the ventral surface of the prothallus. They are of emergent type. The antheridia occur among the rhizoids whereas the archegonia (Fig. 8·17, C) are restricted to the cushion behind the apical notch (*Dryopteris, Pteris, Pteridium, Adiantum, Nephrolepis*). In the filamentous prothalli the sex organs arise laterally on the filaments, but in some cases archegonia are borne on special multicellular cushions.

The endosporic female gametophytes of *Azolla* and *Salvinia* develop several archegonia, whereas those of *Marsilea, Pilularia* and *Regnellidium* bear only one archegonium. The endosporic male gametophytes in *Marsilea* and *Azolla* bear two antheridia and produce 32 and 8 antherozoids, respectively. The endosporic male gametophytes in *Salvinia* produce two antheridia with a total of 8 antherozoids from both.

Structure of sex organs

(*a*) **Antheridium.** In the homosporous ferns the antheridium is a simple object containing a variable number of spermatozoids enclosed by a single layer of wall cells. The number of wall cells varies from 3 to many. In the primitive homosporous groups **Ophioglossales** and the **Marattiales** the antheridia are embedded in the p... which belongs to the advanced grou... embedded (Fig. 8·22, 6-12) ... n the homosporous ferns. These are (*i*) the **eusporangiate antheridia** that are characteristic of the primitive groups, and (*ii*) the **leptosporangiate antheridia** that are found mostly in the advanced groups.

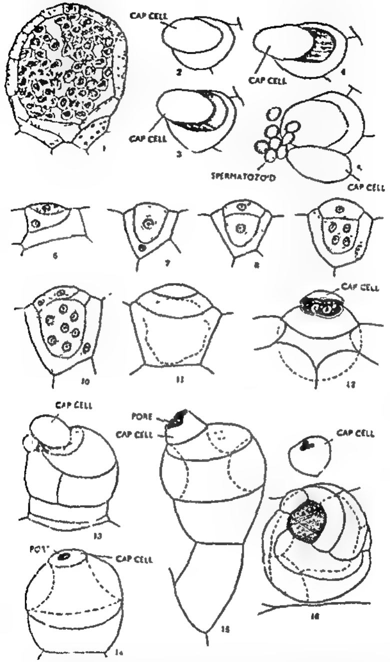

Fig. 8 22. Antheriadia of homosporous ferns.

1. L.S. antheridium of *Todea barbara* (After Stokey) 2—5. Stages in antheridial dehiscence of *Anemia* by slipping of cap cell. 6—12. Stages in the development of antheridium of *Ceratopteris thalictroides*. 11. Lateral view of mature antheridium. 12. Showing dehiscence (After Nayer & Kaur, 1971). 13 Dehiscence of antheridium in *Alsophila excelsa* (After Stokey) 14. Dehiscence of antheridium by apical pore in *Stenochlaena tenuifolia* (After Nayyar and Kaur, 1971). 15. Dehiscence of antheridium in *Cibotium suspensa* by apical pore (After Stokey). 16. Antheridium of *Chieropleuria bicuspis* showing dehiscence by throwing off of cap cell (After Stokey and Atkinson).

In the eusporangiate types the antheridia are large and massive and produce over 100 spermatozoids. They are embedded and are surrounded by a wall consisting of 10—30 narrow and elongated cells. In **Ophioglossales** the wall may become 2—3 cells thick. From one of the wall cells in the anterior part of the antheridium, one or two small triangular or ovate cap cells are cut off. They constitute the **operculum.** The antheridium is attached to the prothallus by two or three wedge-shaped or flat basal cells. During dehiscence the cap cell is thrown off intact to release the spermatozoids.

In the leptosporangiate type of antheridium the wall is made up of three cells : (*i*) the basal cell which may be funnel-shaped (*Dryopteris*, *Adiantum*, etc.), barrel-shaped (*Ctenopteris*) or discoid (*Stenochlaena*) ; (*ii*) the annular or the ring cell ; and (*iii*) the apical cap cell or the cover cell. It encloses 16—32 spermatozoids. During dehiscence the cap cell behaves in the following manner :—

(*a*) In some leptosporangiopsida the cap cell is thrown off (Polypodiaceae) and it often collapses during the process (*Hartman*, 1931), (Fig. 8·22, 16).

(*b*) In Cheilanthaceae and Parkeriaceae the cap cell is lifted like a hinged lid (Fig. 8·22, 12).

(*c*) In *Ctenopteris* and *Stenochlaena* a pore is formed in the cap cell (Fig. 8·22, 14—15) and the sperms are released through it.

(*d*) In *Anemiaceae* (Fig. 8·22 2—5) the cap cell is detached all around and slips off side ways, thus opening up the antheridium.

The heterosporous ferns have antheridia enlosed completely within the microspore wall. The antheridial wall is single layered. Some regard that in *Marsilea* a single male gametophyte has two antheridia because there are two distinct groups of androcyte mother cells. There is no cap or opercular cell in the hetrosporous ferns. The entire jacket disintegrates. This is followed by the dissolution of the microspore wall thus liberating the sperm mass.

(*b*) **Archegonium.** The archegonium in all the ferns is made up of two distinct parts : (*i*) the **neck** and (*ii*) the **venter.** *The* neck is composed of four longitudinal rows of cells, each row *having* an equal number of cells that vary among the ferns. The neck is closed by four cells called the **cover cells** and encloses a neck canal which is filled with one or more **neck canal cells.** *The* **venter** is the lower swollen region of the archegonium and contains a single egg and a **ventral canal cell.** The neck canal cells, the ventral canal [illegible] of cells. The venter is *surrounded* [illegible] at may remain distinct from the [illegible] ay become *indistinguishable.* The archegonia in *Ophioglossum* are embedded in the *tissue of the pro*thallus with only the upper portion of the neck slightly projecting. In *Botrychium* the archegonial neck projects sufficiently *above* the prothallus. The neck in *Ophioglossum* is made up of 4 *longitudinal* rows of cells, each row 3 to 4 cells in height. There is a *single*

binucleate neck canal cell. The same is the case in Marattiales. The archegonial neck is up to 8 cells high in *Osmunda cinnamomea* and projects above the prothallus surface. The archegonial neck in *Gleichenia* (Gleicheniaceae) may be 7-14 cells in height and is always directed towards the growing apex. The neck may be curved or straight. The necks of archegonia in the polypodiaceae are strongly curved away from the apex of the prothallus and may be 3—6 cells in height. In Anemiaceae, Matoniaceae, Gleicheniaceae and Cheiropleuriaceae the archegonial neck is curved towards the apex of the prothallus whereas in others it is curved away from the apex. The former position along with long necks is a primitive condition. The single neck canal cell is binucleate. The archegonia are emergent in ferns with filamentous prothalli. The neck canal cell is binucleate and generally swollen towards the apex at maturity. This is an advanced condition. In Gleicheniaceae, Cyatheaceae, Schizaeaceae and Dicksoniaceae the neck canal cells are sometimes 4-nucleate. In Plagiogyriaceae the neck canal has 4 cells. Nishida and Sakuma (1961) have reported abnormal archegonia with multinucleate and multicellular neck canals and with two ventral canal cells in some primitive families.

The axial row of cells, except the egg or the oosphere, degenerate thus making a passage for the sperms to swim through. The four terminal cells or the cap cells separate from one another and diverge or are thrown away thus opening the archegonial neck. It is probable that the degenerated mass of axial cells absorbs water and swells up thus exerting a pressure on the cover cells. The cover cells may be thrown off or may separate and diverge thus making an open passage. As a result a drop of liquid oozes out through the opening. The exudate contains an organic acid (usually malic acid) or some other substance whose smell attracts the spermatozoids. Under this chaemotactic response the spermatozoids reach the neck, enter it and one of them is able to penetrate the egg cytoplasm and effect fertilization. Ward (1954, pp. 1-17) gives an excellent account of the process of fertilization in *Phlebodium aureum* and Wilkie (1954) studied it in *Pteridium aquilinum*.

Development of sex organs. The mature sex organs (antheridia and archegonia) look strikingly different but they show a remarkable similarity, at least in their early stages of development. Both originate as one-celled protuberances, from the superficial layer of the prothallus. It is very difficult to say, at this stage, as to which will develop into antheridium or an archegonium. There is no morphological or cytological criterion to determine which is which. At this one-celled stage these initials seem to be uncommited. It appears that their nutritional biochemical milieu might be the determining factor guiding their developmental destiny, whether antheridium or archegonium. It seems probable that the genetic system controlling the processes involved can invoke different biochemical path-ways and produce different phenotypic end products.

Archegonium. The Superficial archegonial initial divides first by periclinal wall. This wall separates an outer sterile **primary cover cell** and an **inner cell.** The for mer divides by two interesecting walls to form four cover cells, which further by transverse divisions give rise to 4 longitudinal rows of neck wall. The inner cell may divide transversely into a lower **basal cell** and an upper **central cell** or may function directly as the **central cell.** The central cell is the potential fertile cell which by further transverse divisions gives rise to the neck canal cell, ventral canal cell and the egg. The central cell divides transversly into an upper **primary neck canal cell** and a lower **primary ventral cell.** The former may divide into two or more neck canal cells, but in the ferns it functions directly as the single canal cell that is usually binucleate. The primay ventral cell divides into an upper smaller **ventral canal cell** and a lower **egg cell.**

Nishida and Sakuma (1961) studied archegonial development in a number of homosporous ferns and pointed out that there are variations in the nuclear divisions in the axial row of cells. In *Ophioglossales*, *Adiantaceae*, *Cheilanthaceae*, *Dryopteridaceae*, *Lindseaceae*, *Pteridaceae*, and *Dennstaedtiaceae* the ventral canal cell is differentiated only after the neck canal cell has completed its nuclear divisions. In *Anemiaceae*, *Cyathaeaceae*, *Gleicheniaceae*, *Grammitidaceae*, *Hymenophyllaceae*, *Loxosomaceae*, *Marattideae*, *Osmundaceae*, *Parkeriaceae*, *Plagiogyriaceae*, and *Polypodiaceae* the ventral canal cell is formed before the nucleus of neck canal cell divides. In *Blechnaceae* and *Mattoniaceae* both the conditions are found. They consider this character as of significance in the phylogeny of the ferns.

Antheridium. The eusporangiate type of antheridium develops from a superficial wedge shaped initial that differentiates from a superficial cell of the prothallus. The divisions of the antheridial initial do not follow any regular sequence of cell divisions. Earlier divisions distinguish a central androgonial cell surrounded by many wall cells. The androgonial cell divides repeatedly to form androcytes whose protoplasts metamorphose into spermatozoids.

In the embedded type of antheridium in Ophioglossales and Marattiales the embedded antheridium is of massive eusporangiate type. It originates as a single antheridial cell that is superficial but does not project above the prothallus surface It divides by a transverse wall into a lower **androgonial cell** and an upper **primary cover cell.** The cover cell divides by 3 or 4 vertically intersecting walls to form a row of cover cells Out of these the central cell acts as an **opercular cell** (or cap cell). Sometimes the cover cells divide by a transverse wall so that, this layer becomes two celled thick. The androgonial cell enlarges and divides repeatedly to form a mass of spermatocytes whose protoplasts metaphorse into spermatozoids. As the spermatozoids are developing

the surrounding cells of the prothallus divide to cut off an antheridial wall of 2 or 3 cells thick.

The embedded antheridium of *Ceratopteris* (Fig. 8·22, 6-12) is basically of leptosporangiate type but differs in some respects. In this case a prothallial cell acts as a mother cell and divides by an oblique wall to cut off a wedge shaped **antheridial initial.** The first division in the antheridial initial is by a curved wall that deepens sufficiently (Fig. 8·22, 6-7). It cuts off a peripheral cup-shaped cell surrounding an anterior cell on all sides except the upper flat side. It has a dome shaped base and a flat upper end. The second wall appears in the anterior cell near its upper end. This wall is flat (Fig 8·22, 8) and touches the first wall all around. It separates a large central **androgonial cell** and a flat or discoid peripheral cell. The third wall appears in the flat peripheral cell and is concave touching the upper wall of the androgonial cell (Fig. 8·26, 10). It cuts off a circular cap cell This sequence of development was studied by Nayar and Kaur (1969).

Development of the emergent or projecting type of anthedridium is leptosporangiate and differs considerably from the embeded type. In this type of antheridium the first wall does not set apart a sterile jacket cell and a fertile primary androgonial cell. The formation of the latter is delayed until two or more sterile jacket cells have been cut off The details of development of the emergent type of antheridium have been studied in the polypodiaceous ferns by many workers. The studies reveal certain variations in the laying down of the three walls that lead to the separation of three jacket cells and an androgonial cell. They fall into three categories : (*i*) The classical concept which was upheld by Strassburger (1869), Campbell (1886, 1895, 1905), Atkinson (1894) and Laderberg (1907).

(*ii*) Davie's concept that was put forth by Davie in 1951. It is widely accepted and has been quoted in many texts that appeared after 1951 (Smith, 1955) ; Sporne, 1962 ; Bell and Coombe (1965).

(*iii*) Stone's concept was put forth by Stone (1958, 1961, 1962) as a result of her studies on Blechnaceae, Polypodiaceae and Hymenophyllaceae.

[illegible]

[illegible] cells (basal cell, ring cell, and opercular cell) and an **androgonial cell.** The manner how the three walls are laid down is controversial and has given birth to the above-mentioned three concepts. According to the classical concept the first wall is funnel-shaped (Fig. 8·23, 1—1). It cuts off an outer **first ring cell** and a larger **central cell.** The central cell divides by means of a curved periclinal wall (Fig. 8·23, D, 2-2) into an inner **primary**

androgonial cell and an outer **jacket cell.** The jacket cell divides by a curved anticlinal wall (Fig. 8·23, E, 3-3) into a **second ring**

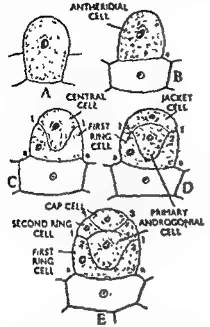

Fig. 8·23. (*A*—E). Illustrating the classical concept of antheridial development in ferns. (Diagrammatic)

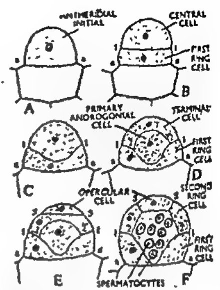

Fig. 8·24. (A—F). Illustrating Davie's concept of wall formation during antheridial development in the polypodiaceae. (Diagrammatic. Adapted from Davie)

cell and an **opercular cell.** Davie (1951) studied the development of antheridium in *Pityrogramma calomelanos* (Adiantaceae) and some species of Polypodiaceae. He challenged the classical concept of the development with regard to the plane of cell division. According to him all the three walls discussed above are laid down in a transverse plane. The first wall (Fig. 8.24, B, 1-1) is flat transverse or slightly curved and never funnel-shaped. It becomes bent downward (Fig. 8.24, *C*) till it touches the basal wall (*a-a*), due to the increasing turgor within the upper cell. According to Davie the primary androgonial cell enlarges and forces the second wall (2-2) into contact with the third wall (Fig. 8.24, *F*). Stone (1958, 1961, 1962) agrees with Davie (1951) that the first wall is trans-

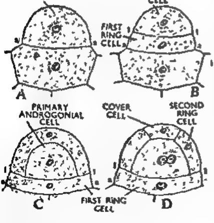

Fig. 8·25 (A—D). Diagrammatic illustration of wall formation in a polypodiaceous fern as observed by Stone. (After Stone)

verse and not funnel-shaped (Fig. 8·25, A—D). Regarding the second wall she disagrees with Davie (1951) and agrees with the classical concept. According to her the second wall is hemispherical and parallel to the outer wall of antheridium (Fig. 8·25, C, 2-2). Verma and Khullar (1966) regard that the third wall is transverse (Fig. 8·26, B) and flat or slightty concave (Fig. 8·26, E) and "is usually in contact with the convexity of the second wall".

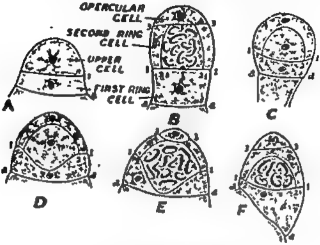

Fig. 8·26 *Adiantum lunulatum* (A—F). Stages in the development of antheridium,
(After Verma and Khullar)

An excellent account of the morphology of the
homosporous ferns was given by
have referred to the nature of th
polypodiaceous ferns. They agre ... (1951) in that the first wall is always flat in the beginning. They have not discussed the second and the third walls. The consensus of opinion now is in favour of the first wall being transverse.

In *Adiantum lunulatum* (Verma and Khullar, 1966) the first wall is transverse and may remain flat (Fig. 8·26, A) or become variously curved (Fig. 8·26, C, D, E) The second wall is always hemispheri-
he third wall may be flat trans-
wall. In some cases the third
(Fig. 8·26, F). In this species
walls. ...ure of the first and the third

EMBRYOLOGY

In filicophyta, rather in all the archegoniate plants, fertilisation or the fusion of the sperm nucleus and the egg nucleus takes place within the venter of the archegonium. Prior to fertilisation certain remarkable biochemical changes have been reported to take place in ferns. Bell (1963) investigated the unfertilised egg or ovum of

Pteridium aquilinum. By using some special staining techniques and autoradiography, Bell demonstrated that the ovum is quite different in cytoplasmic organisation from the surrounding cells of the prothallus. The Deoxyribose nucleic acid was determined to be in stable state in the nucleus and the cytoplasm, except around the nucleus, where it was in higher concentration. The basic proteins and the RNA were present in larger quantities in the ovum cytoplasm than those of the surrounding prothallial cells. During nutrition the nucleus of the ovum was seen to give out small outgrowths or 'blebs' from its periphery into the cytoplasm. This occurred during the outward movement of the nuclear DNA. This study of the ovum reveals that certain significant cytoplasmic transformations occur in the egg, before fertilisation.

As a result of fertilisation a diploid cell called the **zygote** or the **oospore** is established. It is protected by the venter of the archegonium and the [illegible] sue. The earlier stages of [illegible] bryo are effected in this the [illegible] The developing zygote is the pioneer structure of the sporophyte generation. It is held to be a very important and a significant structure. The protoplast of the zygote represents a complicated and a specialised diffusion reaction system. Before it undergoes division, it is now known that special biochemical reactions are initiated in its cytoplasm. These include a patternized distribution of enzymes and metabolites. These biochemical changes are said to guide the future developmental course of the embryo (Rondet 1962) The entire organisation of the future sporophyte plant is designed in the developing zygote. This small structure presents a microcosm of interactions of a complexity equal to or even greater than that of the mature growing plant.

The first prerequisite of the development of zygote into an embryo is the determination of polarity, *i.e.*, the establishment of the base and apex of the embryo. The plane of first division wall in the zygote decides the polarity of the embryo. Three types of polarity have been recognised in the vascular cryptogams. These are:—

(*i*) **Exoscopic** (Fig. 8·27, A). The first division wall in the archegonium is at right angles to the long axis of the archegonium (it may be said to be transverse). The cell nearer to the neck of the archegonium acts at the apical cell and gives rise to the shoot apex The lower cell gives rise to the foot. No suspensor is differentiated. It is characteristic of *Ophioglossum*, *Botrychium simglex*, *B lunaria*, *Azolla* and *Salvinia* *Tmesipteris*, *Psilotum*, *Isoetes* and *Equiselum* are the other pteridophytes in which the polarity is **exoscopic**.

(*ii*) **Endoscopic** (Fig. 8·27, B, C). The first division wall in the zygote is at right angles to the long axis of the archegonium but the cell nearer to the neck of the archegonium acts either as suspensor or it gives rise to the foot. The inner cell acts as the apical cell and gives rise to the shoot apex. Endoscopic polarity is, therefore, of two types (Fig. 8·27, B).

(*a*) **Endoscopic without suspensor.** Such embryos are endoscopic but have no suspensor, *e.g., Marattia* and some related genera, *Kaulfussia, Angiopteris*. The cell nearer to the archegonial neck gives rise to the foot whereas the lower cell gives rise to the shoot apex.

(*b*) **Endoscopic with suspensor** (Fig. 8·27, C). Suspensor and foot are formed near to the archegonial neck, *e.g*, *B. obliquum, Helminthostachys, Danaea, Macroglossum*. In *Angiopteris evecta* sometimes the suspensor is present and sometimes it is absent.

(*iii*) **Lateral** (Fig. 8·27, D). This type of polarity is characteristic of the leptosporangiate serns (*Dryopteris, Adiantum, Pteris, Pteridium, Onoclea, Marsilea*, etc.). The first division wall of the zygote is parallel to the longitudinal axis of the archegonium (Fig. 8·27, D). No suspensor is differentiated out of the two cells thus formed, the one nearer the apex of the prothallus is called the **epibasal cell** and forms the shoot apex and the first leaf. The other cell is the **hypobasal** or the posterior cell and gives rise to the foot and the root. The second wall is at right angles to the first and results in the formation of the quadrant stage (Fig. 8·27, E).

The first division wall of the zygote may divide it into two equal cells or one of the two cells may be smaller than the other. In *Pteris serrulata* the epibasal cell is smaller than the hypobasal whereas in *Marsilea* the hypobasal cell is smaller. This difference in the size of the two cells has been attributed to the cytoplasmic and metabolic differences at the two poles of the zygote (Wardlaw, 1968).

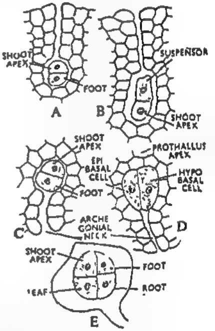

Fig. 8·27. Kinds of polarity in Embryo development in filicophyta. A. Exoscopic; B. Endoscopic with suspensor; C. Endoscopic without suspensor; D. Lateral; E. Quadrant of D.

Early Embryology. The early embryology includes the determination of polarity and early segmentation leading to the establishment of apices of stem, first leaves and root and also the development of foot. Different types of polarity have been discussed in the preceding paragraph. Future segmentation of the two celled zygote will be discussed separately among the eusporangiate and the leptosporangiate ferns.

(*a*) **Eusporangiate ferns** (Eusporangiopsida). The rangiopsida include two orders, *viz.*, the Ophioglossales

Marattiales. The Ophioglossales are represented by the living genera (*Ophioglossum, Botrychium, Helminthostachys*). *Marattia* and *Angiopteris* are the important and widely distributed genera of the Marattiales. A comparative account of earlier stage of embryo development will be given below.

There are slight variations in the earlier and later stage of development of the embryo in various species of Ophioglossum. Based on these variations, Campbell (1911, 1940) recognised three distinct patterns of embryo development in this genus. These are represented by *Ophioglossum vulgatum, O. moluccanum* and *O. pendulum*. In *O. vulgatum* the first wall of the zygote differentiates an epibasal segment nearer to the archegonial neck and a hypobasal segment. The next division leads to the quadrant stage. One of the hypobasal quadrants gives rise to the foot, whereas the endogenous root apex differentiates by the activity of the other hypobasal quadrant. The epibasal quadrants divide into a number of undifferentiated meristematic cells. It remains undifferentiated for several seasons. The first root develops rapidly and grows into the soil. The foot also becomes conspicuous but the epibasal mass of cells remain undifferentiated. At a very late stage of development the shoot apex, the apex of the first leaf and the leaf sheath make their appearance in epibasal half. Later the apex of second root also becomes evident. The second leaf makes its appearance in the epibasal half The vascular strands appear first in root and even in the leaves and become joined. In *O. moluccanum* the hypobasal quadrants of the embryo give rise only to the foot. The epibasal segment gives rise only to the first leaf. The primary root arises endogenously from the middle of the embryo and is not referable in origin to either of the two halves. The shoot apex originates endogenously in the primary root and consists of a group of meristematic cells. The first leaf and the first root almost elongate rapidly at the same time and come out of the prothallial tissue. The second leaf appears close tc [illegible] connection with it. The vascular strand [illegible] of the primary root. [illegible] The epibasal segment gives rise to the root or sometimes to both the first and second roots. The hypobasal segment gives rise to a large and massive foot. The shoot apex makes its appearance very late and appears at the base of the primary root. It is believed that shoot apex becomes organised in the epibasal half but due to slow development it is displaced from its original position by the rapidly developing root.

The protoleptosporangiopsida, that are represented by various species of *Osmunda*, exhibit lateral polarity in their embryos. The development is typically leptosporangiate. The first wall of the zygote is parallel to the long axis of the archegonium. The second wall is at right angles to the long axis of the archegonium and forms a quadrant stage. The four cells of the quadrant stage divide by a transverse wall to form an octant stage. Further divisions do not follow a regular pattern and lead to the formation of a globular

embryo. The primary organs (shoot apex, leaf, root apexand foot) differentiate at a later stage. Gross (1931) studied the embryology in *Osmunda cinnamomea* and described the first leaf, stem and the root are formed from the half of the octant adjacent to the archegonial neck. The foot develops from the entire other half. The first root has an endogenous origin. The foot is massive and bulky (eusporangiate character).

(*b*) **Leptosporangiate Ferns.** The archegonia in the lepto- [illegible] *Adiantum, Onoclea, Pteridium,* [illegible] the lower or the ventral surface [illegible] re curved. The fertilized egg or the zygote is almost spherical in form. The first division wall is parallel to the longitudinal axis of the archegonium (*Fig.* 8·27. D). *Cardiomanes reniforme (Trichomanes reniforme)* is an exception. In this fern the first partition wall is at right angles to the long axis of the archegonium. The second wall in majority of the leptosporangiate ferns is at right angles to the axis of the archegonium and forms a quadrant stage. In *Cyathea* (Stokey, 1930) the first two partition walls in the zygote are vertical. The third one is also supposed to be vertical in *Cyathea*. The third wall in majority of the Leptosporangiate ferns is transverse and forms the octant stage The first leaf, the shoot apex, root and foot are referable in origin from definite portions of the octant stage The first division wall of the zygote in most of the ferns produces two unequal cells (Fig. 8·27 D). The cell towards the apex of the prothallus is known as the **epibasal cell** and is smaller in size (in *Marsilea* it is larger in size) whereas the other one is larger and is called the **hypobasal cell** (Fig. 8·27. D). The earlier workers believed that the primary organs like stem, leaf and root and foot can be definitely traced back to these two segments or to the individual cell of the quadrant stage. According to them the shoot apex and the first leaf develop from the epibasal cell. The foot and the root can be traced back to the hypobasal cell. If we consider the octant stage, with respect to the origin of these four organs, the first leaf originates from the two epibasal octants that lie nearer to the archegonial neck (superior epibasal octants). [illegible]

octant stage is followed by a 16-celled and 32-celled stages. According to Vladesco (1935) the divisions leading to these stages follow a regular sequence. D'Arcy Thompson (1917, 1942) and Thompson and Hall (1933) compare these divisions to walls of minimal [illegible]

1954). Vladesco (1935) reported that in *Gymnogramme sulphurea* the foot is derived partly from the superior epibasal octants and

partly from superior hypobasal octants. The shoot, in this fern, does not develop from the inferior epibasal octants but from the equatorial region of the embryo. The first leaf originates from both the inferior epibasal octants. Ward (1954) stated that in *Phlebodium aureum* the shoot cannot be traced back to any definite position in the embryo. The foot develops from both the inferior quadrants, the leaf from the superior epibasal quadrant and root from superior hypobasal quadrant Lot of variations have been reported in the leptosporangiopsida regarding the origin of primary organs, but fuller details of many of them remain to be worked out. Vladesco (1935) noted some irregularities in the embryology of *Dryopteris filixmas*. The embryology of this species was worked out by Hofmeister, Becquerel (1931) and Vladesco (1935). The first wall, which is usually parallel to the axis of the archegonium, divides the zygote into a smaller epibasal (towards the apex of the prothallus) cell and larger hypobasal cell. The second wall is at right angles to the archegonial axis (Vladesco, 1935) and produces a quadrant stage with unequal cells. The third wall is transverse and leads to the octant stage. The organs make their appearance in the post-octant stage. There is some difference in their inception as compared to other leptosporangiopsida. The foot develops from the superior epibasal and hypobasal octants. The root arises from the equatorial region of the embryo. The root initial cannot be assigned definite position in the octants. The first leaf arises from the inferior epibasal octants. Such irregularities, as described above, have also been noted in *Pteridium aquilinum*. Valdesco (1935) is of the opinion that octants have no organogenic significance. Vladesco (1931) reported two embryos developing in one archegonium of *Dryopteris parasitica*.

EVOLUTIONARY TRENDS AMONG THE FILICOPHYTA

A comparison of the living and fossil genera led Bower (1923) to make a list of certain primitive characters of the ferns. Holttum (1947) and Stokey (1951) modified Bower's list and enumerated them as follows :—

1. The prostrate, creeping and slender rhizomes showing dichotomous branching are considered to be primitive than the oblique and upright rhizomes.

2. Rhizomes with leaves arranged in two distinct rows are regarded as primitive than those without any definite arrangement.

3. Protostelic rhizomes are primitive.

4. Rhizomes covered with hair are primitive as compared to those that are covered with ramenta and scales.

5. Ferns with large and dichotomously branched leaves are primitive.

6. Ferns with leaves having unlimited growth are primitive.

7. Open and furcate venation is primitive.

8. A single leaf trace entering the petiole is a primitive condition.

9. Sori with few sporangia are primitive.

10. Sori terminating a vein are primitive.

11. Gradate sori are primitive as compared to mixed type.

12. Massive sporangia are primitive.

13. Sporangia with short and thick stalk and many layred wall are primitive

14. Sporangia without annulus are primitive.

15. Sporangia with large number of spores are primitive.

16. Amorphous type of spore germination is primitive.

17. Tuberous and endophytic prothalli are primitive.

18. Long lived prothalli are primitive.

19. Archegonia with long necks are primitive.

20. Antheridia with many celled wall are primitve.

21. Archegonia with necks pointed towards apex are primitive as compared with those with necks facing posterior side.

22. Antheridia with large number of spermatozoids are primitive.

[illegible]

families in the centre (Fig. 8.28) of the circle with an advancement index a little above zero. The most advanced families were placed in outermost circle with an advancement index as hundred or cent per cent. Those with advancement indices 20, 40, 60 and 80 are placed between zero and 100 (Fig. 8·28). He regarded the *Schizaeaceae* and the *Gleicheniaceae* as the two primitive most families. *Hymenophyllaceae, Dicksoniaceae, Mattoniaceae, Dipteridaceae* and *Dannstaedtiaceae* come next. The first one has an advancement index of twenty, whereas the others have 40. Similarly those in outer circles have 60 and 80 as advancement indices (See Fig. 8·28). The broken line indicate the close relationship and the affinities of the various families.

The points given above regarding the determination of primitive and advanced types are in no way final and have been changed by subsequent workers. The recent trends of evolution will be outlined at the conclusion of this discussion Recent cytotaxonomical studies supported by anatomical data, ecological variations, and specific biochemical data and physiological data should all be taken into account to decide the phylogeny of the group. The above scheme has not even taken into consideration features of interest, presented by gametophyte and embryo.

Wagner (1952-54) has discussed the problem of divergent evotution in the genus *Diellia* and of reliculate evolution in *Asple-*

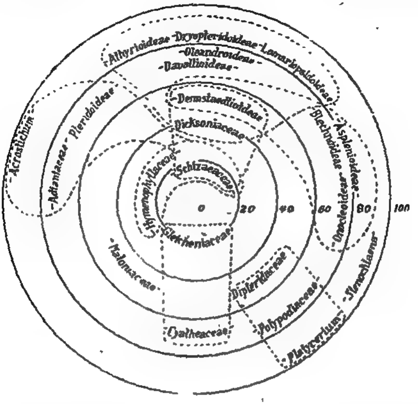

Fig. 8.28. *Sporne's scheme of circular phyllogenetic classification of the filicales (After Sporne).*

nium. His conclusions, are sound and are based on cytological, ecological and anatomical data. His conclusions were also confirmed by the chemical data obtained in the Appalachian species of *Asplenium* by D.M. Smith and Levin (1961).

Mehra (1961) discussed the cytological evolution of ferns with special reference to the Himalayan ferns. He suggested a phylogenetic scheme of evolution among the ferns (Fig. 8.29). He based his ideas on the data available from morphology, anatomy and cytology of as man; ... the ferns in India. He recognised six stocks whi ... to them. The ... *Schizaeace* ... states, "I ... of years of ... of ferns as we see ... evolution many of the intermediate stages have been ... at we see today are merely the end points and in some cases relics of a long process of differentiation".

The Ophioglossaceous, Marattiaceous, and the Osmundaceous

stocks evolved into the families Ophioglossaceae, Marattiaceae and the Osmundaceae, respectively. Thereafter they ended blindly. The Ophioglossaceae have no known fossil history but according to Prof. Mehra (1961, 147, 148) the highest chromosome number of some species (O. reticulatum, $2n=1260$) speak of its antiquity. The Marattiaceae were represented by some fossil genera in Palaeozoic. Their basic number as evidenced by haploid chromosome counts of two of the living genera *Marattia* and *Angiopteris* ($n=40, 78$; $n=40$ respectively) seems to be 10. Likewise the Osmundaceae were also represented in the Palaeozoic by some genera such as *Zalesskya* and *Thamnopteris*.

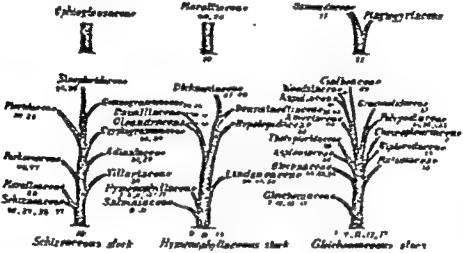

Fig. 8·29. Prof. Mehra's phylogenetic scheme of evolution among the ferns. (After Prof. P.N. Mehra)

The Schizaeaceous stock diverged into nine families. The basic chromosome number of this stock is 10. Majority of the families have a monoploid number 30 and 29. A few like *Marselia* have 20 and *Ceratopteris* is $n=40$. Both are reduceable to 10. Mehra believed that the number 29 must have been derived from 30. The families derived from this stock are named in Fig. 8·29. Marsileaceae is believed to have originated as an offshoot that adapted to aquatic habitats and developed heterospory. Parkeriaceae is also considered to be a specialised side line that took to the aquatic mode of life, but resembled other members in the characters of spores. The Vittariaceae is also kept apart due to the position of sori and the peculiar gametophytes that are quite different from other members of this alliance. The Gymnogrammaceae are regarded as an offshoot from Sinopteridaceae. The other families included in this alliance are Adiantaceae, Cryptogammaceae, Pteridaceae and Schizaeaceae. The families evolved from this stock had marginal and intramarginal position and were protected by a false indusium (Adiantaceae, Pteridaceae).

The Hymenophyllaceous stock fanned out into 8 families and is characterised by a marginal sorus protected by a bilabiate true

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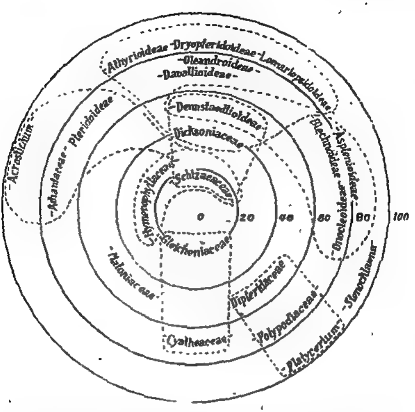

Fig. 8·28 Sporne's scheme of circular phyllogenetic classification of the filicales (After Sporne).

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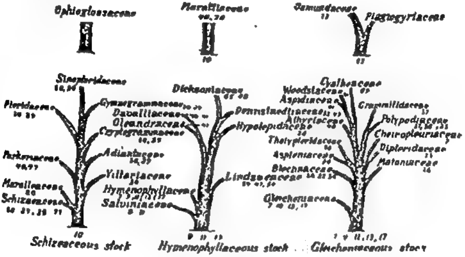

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The Gleicheniaceous stock with basic numbers varying between 7, 9, 11, 13 and 17 fanned out to give rise to 13 families (see Fig. 8 33).

Recently after considering a number of morphological features of the sporophyte and the gametophyte, Bierhorst (1971), Nayar and Kaur (1968, 1969, 1971) and others pointed out a number of characters that can decide the phylogenetic position of a taxon. These have been discussed in detail in the proceeding pages. Here only a complete list of such factors is given.

Primitive features. 1. Terrestrial habitat; plants small in size and with horizontal or upright, short stems. 2 Leaves are poorly differentiated from the stem. 3. Leaves pinnate and limited in growth. 4. Dichotomously veined leaves. 5. The leaf has apical cell with three cutting faces. 6. The leaves have discontinuous marginal meristematic patches that are situated at vein ends. 7. Leaf arrangemer [illegible] of one type. 9. [illegible] simple trichomes [illegible] eloped. 12. Stem is protostelic. 13. Xylem is mesarch. 14. Large simple and adaxially curved leaf traces. 15. Sori are distinct, terminal or marginal in position. 16. Sori elongate. 17. Sporangial maturation in a sorus is gradate or simultaneous. 18. The sori are exindusiate. 19. Sporangia are large and bulky. 20. Sporangia produce numerous spores. 21. Sporangial walls many layered. 22. Spores are monolete. 23. Sporangia have massive stalks. 24. Annulus absent or apical or sub-apical in position. 25. Dehiscence is longitudinal. 26. The line of dehiscence is not regular and anatomically specialised. 27. The spore germination is amorphous. 28. The growth of the prothallus . in by a distinct apical cell or meristem. 29. The prothallus is tuberous, large and subterranean. 30. The prothallus is endophytic and slow in development. 31. The prothallus is devoid of hair and trichomes. 32. The prothallus bears septate rhizoids. [illegible] The anth[illegible] large and produce many spermatozoids [illegible] is many celled. 35. The opercular [illegible] 36. The archegonia have long necks [illegible] 37. The necks of archegonia are ben[illegible] thallus. 38. The zygote divides first [illegible] Embryo is exoscopic. 40. The embry[illegible] leaves. 41. The em[illegible]s a massive

Advanced Features: 1. The plants have long and creeping stems. 2. Epiphytic habit. 3. Leaves are quite distinct from the stem. 4. The leaves are simple and indeterminate. 5. The leaves have reticulate venation. 6. The leaf apical cell has two cutting faces. 7. The leaves have a continuous and uniform marginal meristem. 8. The leaves have a regular arrangement. 9. The leaves may be dimorphic. 10. The stem branching is lateral. 11. The stem bears multicellular, branched and complicated trichomes. 12. The stem has well developed roots. 13. The stele is siphonostelic or solenostelic or dictyostelic. 14. Xylem is exarch. 15. Leaf traces may be multiple or double or treble. 16. Sori are superficial and extend along the veins; they may form censori or may be acrosticoid. 17. Sori indusiate. 18. Sporangia in sorus m

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nulus interrupted by a stomium. 24. Dehiscence is transverse. 25. Dehiscence lines anatomically distinct. 26. Spores trilete. 27. Spores germinate to produce a filamentous protonema. 28. Prothallus growth is diffuse or by lateral or intercalary meristem. 29. The mature thallus is either cordate or strap-shaped or ribbon like. 30. The mature thallus is covered with hair or trichomes of diverse types 31. The prothallus is not endophytic and its growth is quick. 32. The prothallial rhizoids are nonseptate. 33. The antheridia are small and produce only a few spermatozoids. 34. The antheridial wall is 3-celled. 35. The opercular cell is terminal. 36. The archegonia have short, curved necks. 37. The necks are bent towards posterior side of the prothallus. 38. The zygote divides first by a longitudinal wall. 39. Embryology is endoscopic. 40. The embryo has distinct roots and leaves. 41. The foot is poorly developed.

Surgical Experiments: One of the recent trends in the ... cise the zygote or young embryo ... surrounding prothallial tissue and ... Some such expriments have been carried out on leptosporangiate ferns.

Ward and Wetmore (1954) incised the prothallus of *Phlebodium aureum* near the apex of the fertilised archegonial neck. This partial release of the embryo from the surrounding tissue, induced certain changes in developmental pattern of the embryo The young embryo came out of the calyptra (archegonial neck) and developed into an undifferentiated mass of cells. It had no definite shape. The growth was slow. Later it differentiated into stem, leaf and foot, but developed no root. So one significant effect of such a partial isolation from the gametophyte tissue is the formation of rootless embryos. In some cases the embryos developed into irregular, amorphous, tuberous and nonvascularised masses. Such an embryonal mass was observed to give rise to three rootless plantlets.

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The Gleicheniaceous stock with basic numbers varying between 7, 9, 11, 13 and 17 fanned out to give rise to 13 families (see Fig. 8·33).

Recently after considering a number of morphological features of the sporophyte and the gametophyte, Bierhorst (1971), Nayar and Kaur (1968, 1969, 1971) and others pointed out a number of characters that can decide the phylogenetic position of a taxon. These have been discussed in detail in the preceeding pages. Here only a complete list of such factors is given.

Primitive features. 1. Terrestrial habitat ; plants small in size and with horizontal or upright, short stems. 2. Leaves are poorly differentiated from the stem. 3. Leaves pinnate and limited in growth. 4. Dichotomously veined leaves. 5. The leaf has apical cell with three cutting faces. 6. The leaves have discontinuous marginal meristematic patches that are situated at vein ends. 7. Leaf arrangement is irregular. 8. The leaves are monomorphic, *i.e.*, of *one* type. 9. Stem branching is dichotomous. 10. Stem bears simple trichomes or hair. 11. Roots either absent or poorly developed. 12. Stem is protostelic. 13. Xylem is mesarch. 14. Large simple and adaxially curved leaf traces. 15. Sori are distinct, terminal or marginal in position. 16. Sori elongate. 17. Sporangial maturation in a sorus is gradate or simultaneous. 18. The sori are exindusiate. 19. Sporangia are large and bulky. 20. Sporangia produce numerous spores. 21. Sporangial walls many layered. 22. Spores are monolete. 23. Sporangia have massive stalks. 24. Annulus absent or apical or sub-apical in position. 25. Dehiscence is longitudinal. 26. The line of dehiscence is not regular and anatomically specialised. 27. The spore germination is amorphous. 28. The growth of the prothallus is by a distinct apical cell or meristem. 29. The prothallus is tuberous, large and subterranean. 30. The prothallus is endophytic and slow in development. 31. The prothallus is devoid of hair and trichomes. 32. The prothallus bears septate rhizoids. 33. The antheridia are large and produce many spermatozoids. 34. The antheridial wall is many celled. 35. The opercular cell of antheridium is lateral 36. The archegonia have long necks with many neck canal cells. 37. The necks of archegonia are bent towards the apex of the thallus. 38. The zygote divides first by a transverse wall. 39. Embryo is exoscopic. 40. The embryo is devoid of roots and leaves. 41. The embryo has a massive foot.

6. *Cheilanthes.* The Santals prescribe a preparation from the roots of *C. tenuifolia* for sickness attributed to witchcraft or the evil eye.

7. *Drynaria.* The plant of *D. quercifolia* is used in Pthisis, dyspepsia and cough. Its fronds are used as poultic for subsiding swellings. Aqueous extracts have antibacterial properties.

8. *Dryopteris.* The rhizomes of *D. barbigera, D. blanfordii, D. filix-mas D. marginata, D. odontoloma* and *D. schimperiana* possess anthelmintic properties. All of them yield Filicin.

9. *Lygodium.* The plant of *L. flexuosum* of *L. japonicum* is used as an expectorant. The roots of *L. flexuosum* are boied with mustard oil and applied to carbuncles and used externally in rheumatism.

10. *Ophioglossum.* The plant of *O. vulgatum* is used as vulnerary and to heal wounds.

11. *Polypodium.* The rhizomes of *P. vulgare* are purgative.

12. *Pteridium.* The rhizomes of *P. aquilinum* are anthelmintic and astringent.

13. *Sphenomeris.* The plant of *S. chusana* is used internally for chronic enteritis.

14. *Pleopeltis.* Tea prepared from the leaves of *P. lanceolata* is used to cure itch in Mexico. In India it grows in Assam, Western Ghats, Nilgiris and Tamilnadu State.

15. *Osmunda.* The plant of *O. regalis* is used as styptic and for rickets in England.

The rhizones of *Dryopteris filix-mas* and rhizomes and roots of *Polypodium vulgare* yield essential oils. Those of latter also yield a fatty oil that is purgative; a kind of resin and saponine.

M. K. Kshirsagar and A. R. Mehta from Baroda have been successful in isolating antibacterial elements from some ferns from Gujarat (Abstract, Proc. Ind. Nat. Sci, Cong 1973).

[illegible] not lag behind other groups of [illegible] A number of ferns are grown [illegible] beautiful foliage. The following are some of the most common ornamental ferns :

1. *Adiantum.* It is also known as the 'Maiden-hair Fern' and is an excellent pot fern. They [illegible] Some species are also [illegible] attractive and ornament[illegible] *[illegible]eum, A. le-grande, A.* [illegible] *concinnum, A. victoria*[illegible] *A. macrophyllum.*

2. *Alsophila.* It is also called the Grove-Fern and is grown as an ornamental tree fern in spacious gardens. *Alsophila latibrosa, A. australis* and *A. excelsa* are some of the handsome species.

3. *Anemia.* It is also called the Flower fern which is generally grown in flower pots. *A. rotundifolia* is commonly grown in the gardens.

4. *Asplenium.* It is very attractive fern. *A. formosum, A. lunulatum, A. dimorphum* and *A. nidus-avis* are some of the attractive species.

5. *Blechnum* It is also known as the Brazilian Tree Fern and bears palm like leaves. *B. cartilagenium* and *B. occidentale* are grown as indoor species.

Jayasekera and Bell (1959) obtained similar results with another fern *Thelypteris palustris*. Thompson (1934) induced changes in the shape of the foot in the excised embryos of *Marsilea*. Experiments on *Pteris longifolia* by Rivieres (1959) also yielded rootless embryos. He isolated, under aspetical conditions, the archegonia containing fertilised eggs and grew them on Knop's medium He concluded that prothallus tissue has a profound influence on the development of the embryo. It releases certain root forming factors.

The experiments lead us to conclude that the normal tissues surrounding the embryo have a profound influence on its development. The complicated reaction system operating within the zygote has a remarkable power of flexibility. In spite of the various biochemical and experimental studies on the embryology of plants and structure of the zygote, it has not yet been possible for the botanists to unravel the nature of the internal organisation of the zygote, the biochemical changes that take place during the early stages of embryology and the numerous physical factors concerned in the development and segmentation pattern of the embryo. Intensive experimental work is needed to solve the problems. Detailed observation on the development of embryo in Hymenophyllaceae and Schizaeaceae with filamentous prothalli will reveal the effect of surrounding prothallial tissue on the embryology. In some species of *Schizaea Trichomanes* the prothallus is a unseriate and branched filament with archegonia borne on specialised branches called the archegoniophores. They are not surrounded by much of prothallial tissue. The developing embryo is covered only by calyptra. Their detailed embryology can throw some light on the relationship between the development of embryo and the surrounding prothallial tissue.

[illegible] investi- [illegible] omoeo- [illegible] stively.

1. *Actinopteris dichotoma* — It grows throughout India below 4,000 feet especially in dry rocky places. The plant is used as styptic and anthelmintic.

2. *Adiantum* About eight species are medicinally important. The fronds of *A. caudatum* are useful for skin diseases, diabetes, cough and [illegible] diuretic, resolvent, expectorant, and [illegible]

3. *Athyrium*. *A. filix-femina* has astringent rhizomes. The decoction of rhizome and fronds is given in chronic disorders arising due to obstruction of of viscera and spleen.

4. *Blechnum* The plant of *B orientale* is used as a poultice for boils in Malaya.

5. *Botrychium*. The plant of *B. lunaria* is used in dysentery and as a good vulnerary. The fleshy roots of *B. virginianum* are used in application to cuts and bruises.

6. *Cheilanthes.* The Santals prescribe a preparation from the roots of *C. tenuifolia* for sickness attributed to witchcraft or the evil eye.

7. *Drynaria.* The plant of *D. quercifolia* is used in Pthisis, dyspepsia and cough. Its fronds are used as poultic for subsiding swellings. Aqueous extracts have antibacterial properties.

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M. K. Kshirsagar and A. R. Mehta from Baroda have been successful in isolating antibacterial elements from some ferns from Gujarat (Abstract, Proc. Ind. Nat. Sci, Cong. 1973).

ORNAMENTAL FERNS. The ferns do not lag behind other groups of plants in appealing the aesthetic sense of man. A number of ferns are grown in fern houses and in private gardens for their beautiful foliage. The following are some of the most common ornamental ferns :

1. *Adiantum.* It is also known as the 'Maiden-hair Fern' and is an excellent pot fern. They are grown in ferneries, gardens and in the verandahs. Some species are also used for internal decoration. Some of the common attractive and ornamental species are : *Adiantum tenerum, A. flexum, A. formosum, A. le-grande, A. cuneatum, A. decorum, A. aethiopicum, A. bauseii, A. concinnum, A. victoriae, A. peruvianum, A. villosum A. lawso ianum, A. macrophyllum.*

2. *Alsophila.* It is also called the Grove-Fern and is grown as an ornamental tree fern in spacious gardens. *Alsophila latibrosa, A. australis* and *A. excelsa* are some of the handsome species.

3. *Anemia.* It is also called the Flower fern which is generally grown in flower pots. *A. rotundifolia* is commonly grown in the gardens.

4. *Asplenium.* It is very attractive fern. *A. formosum, A. lunulatum, A. dimorphum* and *A. nidus-avis* are some of the attractive species.

5. *Blechnum.* It is also known as the Brazilian Tree Fern and bears palm like leaves. *B. cartilagenium* and *B. occidentale* are grown as indoor species.

6. *Davallia.* It is commonly known as the Hare's Foot Fern and includes many ornamental species, *e.g., D. bullata, D. fijiensis, D. strigosa* and *D. tenuifolia.*

7. *Gymnogramma.* They are also called the Gold and Silver Ferns because the ventral surfaces of some species are covered with yellow or white dust or powder, *e g., G sulphurea, G. chrysophylla, G. tartorea* and *G. pulchella.*

Lomaria (L. gibba), Lygodium (L. scandens, L. palmatum, L. japonicum, L. circinatum), Nephrodum (N. cuspidatum, N. setigerum, N. molle); Nephrolepis (N acuminata, N. cordifolia, N. mucosa, N. rufescens); Onychium (O. japonicum), Pellaea (P. cordata, P. falcata, P. geraniaefolia); Platycerium (P. alicorne) and Pteris (P. cretica, P. vittata, P. ludens, P. serrulata, P. argyraea, P palmata, etc.) are some other ornamental genera of the ferns that are grown in India for their beautiful foliage and elegant posture.

CLASSIFICATION

History. Linnaeus (1753) grouped the Pteridophytes under the order **filices** of the class Cryptogamia. He described 12 genera and 192 species. He treated *Equisetum, Marsilea, Pilularia* and *Isoetes* as fern allies *Lycopodium* was put under the order **Musci.** Linnaeus based his classification on the position and structure of sori. He did not consider the presence or absence of indusium as of any importance.

Adanson (1793) regarded indusium as an important character and formed two series : (*i*) *Indusiatae* which included all those genera in which the *sori* were covered with indusium and *Ex-indusiatae* which included genera with naked sori. J.E. Smith (1793) regarded the presence or absence of annulus as an important character and divided the Pteridophytes into two series (*i*) **Annulatae** and (*ii*) **Exannulate.**

[illegible] divided the ferns into three orders [illegible] ich was further divided into two su[illegible] (*ii*) **Spurie Gyratae,** which includ[illegible] *Osmundaceae, Gleicheniaceae* [illegible] included the families [illegible] iera and 710 species of [illegible] (1828). Kunze (1840)

Presl C.B. (1836) published his classification in '**Tentamen Pteridographie**' created many new genera and species largely based on the type [illegible] ascular bundles entering the petiole. [illegible] described a number of new species [illegible] he *Polypodiaceae* into two divisions : [illegible] George Mettenius (1856) took into [illegible] atomical and soral characters and proposed his classification that was left incomplete by his death in 1866.

Later Diels in the 4th volume of *Engler* and **Prantl's Die naturlichen Pflazenfamillien** (1899) gave an enumeration of all known ferns.

Carl Christensen (1905-06) published a complete enumeration of fern genera and species (149 genera and 6,000 species). Bower (1923) published his three monumental volumes entitled **Filicales** and gave an excellent account of the ferns. He considered that besides soral characters, the structure and the ontogony of the dermal appendages, the venation, the stelar organisation, etc., were also important in *classifying* the ferns. Bower, however, did not propose any new classification. Copeland, E.B. (1929) tried to arrange, in a phyletic sequence, most of the polypodiaceous genera, but his work is incomplete because he has left many African and American genera.

Carl Christensen (1938) published his new phyletic *scheme in* "Manual of Pteriodology" and has tried to include most of the fern species that now number about 10,000. He included all the ferns in class **Filicinae** and divided it into two series (*i*) series Filices

Eusporangiatae and *(ii)* series Filices **leptosporangiatae.** The outline of his system is given below.

CLASS : FILICINAE

1. Series **Filices Eusporangiatae** It included two orders and three families.

Order I. **Ophioglossales**

Family: **Ophioglossaceae** : It included the genera : *Ophioglossum*, *Botrychium* and *Helminthostachys*. The family is characterised by terrestrial sporophytes that are herbaceous and short in size The rhizome is short and fleshy, bearing adventitious roots which may bear adventitious buds *(Ophioglossum)*. Leaves not circinately coiled in bud state, are exstipulate. The fertile leaves have a common petiole that bears a sterile undissected or dissected blade and a fertile spike with marginal sporangia. Spore output is large and may be up to 2,000 spores in a sporangium. They are homosporous. The prothalli are usually underground and mycorrhizic. They are monaecious.

Order **Marattiales.** It includes two families.

Family 1 : **Angiopterideceae** : Sori linear, biseriate ; indusium false, sporangia with rudimentary annulus at the top. Leaves pinnately compound with free veins. It includes the genera : *Angiopteris*, *Macroglossum* and *Pseudomarattia*.

Family 2 : **Marattiaceae** Sporangia fuse to form synangia. Annulus rudimentary. It includes seven genera and about 80 species grouped in three sub-families. The important genera are *Marattia*, *Christensenia* and *Danaea*.

Series II. **Fillices Leptosporangiatae** : It includes two orders :—

1. Order **Filicales** The order includes all homosporous ferns with leptosporangiate development of sporangia and sex organs. The leaves are circinately coiled in bud condition Marsileaceae is an exception because here the spores are heterosporous. It includes the families :

[illegible]
niacea [illegible]
Plagic [illegible]

The famil[illegible] nto fifteen subfa[illegible] loideae (*Nephrole*[illegible] [illegible]*eridium*, *Pteris*, e[illegible] ; Vittaroideae ([illegible]. Woodsioideae ; Dryopteridoideae (*Dryopteris*, *Polystichum*, *Cystopteris*) ; Dipteridoideae; Polypodiodeae (*Pleopeltis*, *Drynaria*, *Polypodium*), and Elaphoglossoideae (*Elaphoglossum*.

2. Order **Salviniales.** It includes the heterosporous water ferns that have sporangia arranged in a basipetalous manner ; have globose and indusiate sori. There is no annulus in sporangia. Leaves are not circinate in bud condition. The microsporangia have numerous microspores. The megasporangia have usually one megas.

pore. It includes the families ; Salviniaceae (*Salvinia*) and Azollaceae *Azolla*).

Reimers (1954) classified the ferns as follows:

Class : Filices : It is divided into 4 sub-classes :—

1. Sub-class : **Primofilices,** which includes all fossil ferns.
2. Sub-class : **Eusporangiatae,** which includes eusporangiate ferns.
3. Sub-class : **Osmundidae** including *Osmunda*.
4. Sub-class : **Leptosporangiatae** includes all leptosporangiate ferns.

Pichi-Sermolli (1959) included the ferns in a class called **Filicopsida,** which is further subdivided into seven sub-classes: (*i*) **Primofilicidae** which includes all the extinct ferns; (*ii*) **Ophioglossidae,** (*iii*) **Marattidae,** (*iv*) **Osmundidae**; (*v*) **Filicidae**; (*vi*) **Marsileidae** ; and (*vii*) **Salviniidae.**

The system of classification that is being followed in this text includes all the ferns in a single order called the **Filicophyta** or **Pterophyta.** It is classified thus.

Order **Filicophyta**

1. Class : **Primofilicopsida** that includes all extinct genera.
2. Class : **Eusporangiopsida** that includes all eusporangiate ferns.
3. Class : **Protoleptosporangiopsida** includes the Osmundales.
4. Class : **Leptosporangiopsida** includes all leptosporangiate ferns that have been discussed in chapters 10—11.

CHAPTER IX

CLASS EUSPORANGIOPSIDA

The eusporangiopsida include the primitive ferns that are characterised [illegible] fertile primary **androgonial cell.** The antheridia produce larger number of multiflagellate spermatozoids. Embryogeny may be **exoscopic** or **endoscopic** with or without suspensor. The gametophytes are long lived and are attacked by an endophytic fungus. They may be colourless; subterranean and saprophytic (*Ophioglossum, Botrychium*) or green aerial and photosynthetic (*Marattia*). The leaves are not circinately coiled in bud conditions (Ophioglossales) and may be stipulate or exstipulate.

The class includes two orders : (*i*) Ophioglossales and (*ii*) Marattiales.

Order : **Ophioglossales**
Family : **Ophioglossaceae**

The family includes 4 genera (*Ophioglossum, Botrychium, Helminthostachys* and *Rhizoglossum*) and seventy species (Willis 1966) of terrestrial and herbaceous plants that have no fossil history. The sporophytes have short reduced and fleshy rhizomes that are devoid [illegible] *Ophioglossum* is [illegible]

OPHIOGLOSSUM L.

Distribution

It [illegible] that achieves luxuriant d[illegible]s occur in the temperate z[illegible] in existence except for two [illegible] *O. pendulum*). The

terrestrial species grow well in soils rich in humus. A few specie *e.g*, *O aitchisoni* (Fig. 9·1) and *O. vulgatum* (Fig. 9·2) have bee

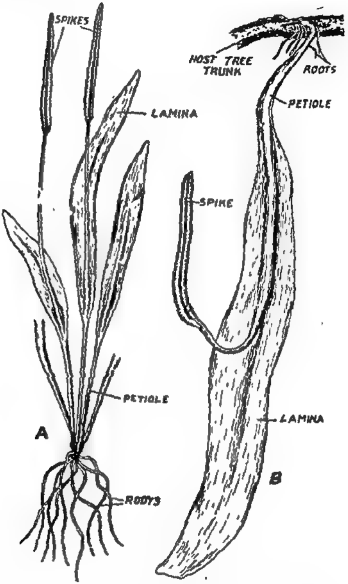

Fig. 9 1 (A—B). A. A complete plant of *O. aitchisoni* showing polyphyllous habit. B. Epiphytic plant of *O. pendulum*.

found growing in clayey soils with a mixture of sand. They are the common Indian species. *The latter species frequents banks of rivers, streams, pools, ponds, and other water courses. It has been reported from many places in N. India and occurs in abundance from* Chamba to Sikkim, ascending up to 9,000 feet. Along the eastern Himalayas it grows luxuriantly at Mount Hattu, 2,000 feet below Darjeeling. In Chhota Nagpur it grows well on Paras Nath Hill at 2,500 feet. It flourishes well in rainy season and early winter (July—November) and

again reappears is spring. It slows down in growth during cold winter months. *Ophioglossum aitchisoni* also grows well during the

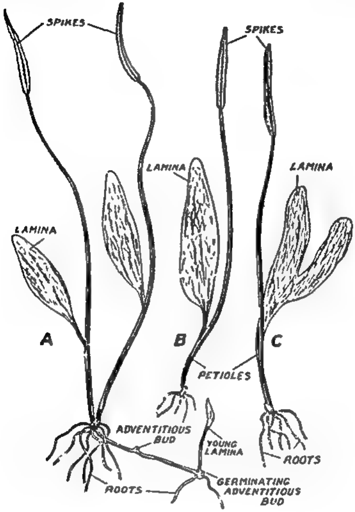

Fig. 9 2. (A—C). *O. vulgatum.*
A. A plant with rhizome bearing germinating root bud. B. A complete plant : C. A plant with divided leaf blade.

rainy season, *i e.*, during July and August. It starts disappearing in mid-September and no trace of the plants is left in the winter and hot summer months. *O. nudicaule* grows in Bangalore, Belgaum, Palghat, Velli, Palai and Kumbanad. Of the two common [illegible]
It is hig[illegible]
tropical [illegible]
depends [illegible]

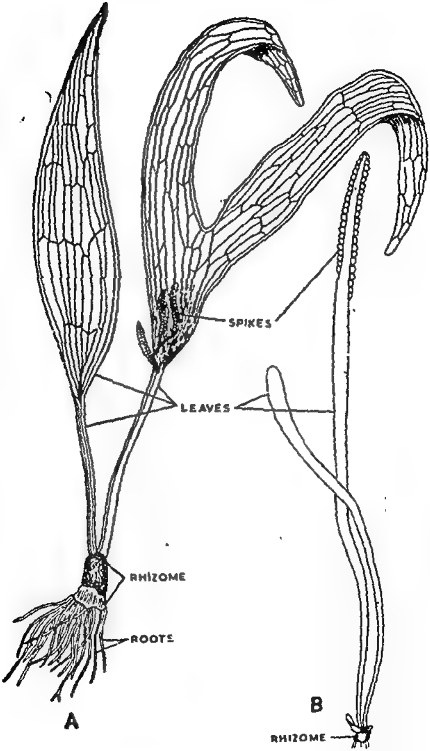

Fig. 9 2 a. *Ophioglossum.*
A. *O. palmatum* showing upright and thick rhizome that stores food. B. *O. simplex* with reduced rhizome and two leaves that have extremely reduced lamina.
(A. after Lawson ; B. after Ridley)

The genus *Ophioglossum*, according to Reimers (1954) includes 45 species. Christensen (1938) recognised 50 species. Bower (1926), Eames (1936) and Clausen (1938) recognised 43, 30 and 28 species, respectively. The total number of species reported from India are a little more than twelve. A few common species are *O. aitchisoni*, *O. nudicaule*, *O. reticulatum*, *O. petiolatum*, *O. pendulum*, *O. gramineum*, *O. lusitanicum*, *O vulgatum* and *O. costatum*. Majority of the species (about 46) are incuded under the sub-genus *Euophioglossum*. *Ophioglossum palmatum* has been included under the sub-genus *Cheiroglossa*. The sub-genus *Ophioderma* includes three species. Such a subdivision of the genus is not followed in many texts.

External features of the sporophyte

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Stem. The rhizome (Figs 9·1 and 9·2) is usually short, cylin-

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gatum and *O moluccanum*. The rhizome is short and thick in *O. palmatum* (Fig 9·2 *a*, A). It is very much reduced in *O. simplex*

a dorsi-

it Petry

Leaf. The sporophytes may be monophyllous or polyphyllous. *Ophioglossum vulgatum* (Fig. 9·2) and *O. molucannum* are ordinarily monophyllous, *i e.*, only one leaf unfolds during one growing season, but two or even three leaves have also been reported to spring up in one season (Fig. 9 2, A). *Ophioglossum aitchisonii* and *O. lusitanicum*

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developed and

species is characterised by the presence of several spikes that are arranged in two rows along the margins of the basal portion of the palmate lamina and the distal portion of the petiole. The leaf reaches its maximum size in the epiphytic *O. pendulum* (about 1·5 metres), where it has short petiole that merges insensibly into a branching and narrow strap shaped lamina (Fig. 9·1, B). The venation is reticulate but a distinct midrib (Fig. 9·1, B) is lacking.

Root. [illegible] roots arise from the rhizome and may be branch[illegible] bear root hair and are heavil[illegible] It has been observed that o[illegible] origin of a leaf or opposi[illegible] leaves. The roots of many [illegible] into new plants and serve [illegible] 9·2 A).

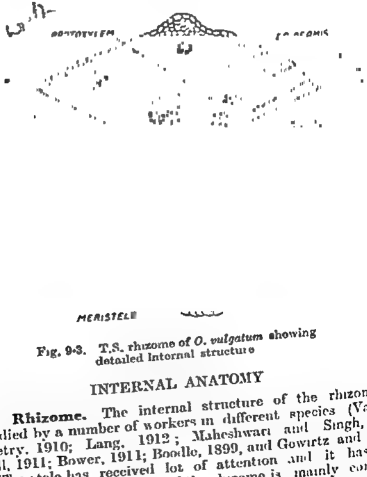

Fig. 9·3. T.S. rhizome of *O. vulgatum* showing detailed internal structure

INTERNAL ANATOMY

A. **Rhizome.** The internal structure of the rhizome has been studied by a number of workers in different species (Vasishta, 1927; Petry, 1910; Lang, 1912; Maheshwari and Singh, 1934; Campbell, 1911; Bower, 1911; Boodle, 1899, and Gowirtz and Fahn, 1960). The stele has received lot of attention and it has been ascertained that the vasculature of the rhizome is mainly composed of a meshwork of root traces and leaf traces. A transverse section of the rhizome reveals an irregular outer contour. This is due to the presence of numerous leaf bases and adventitious root bases. There is a distinct outer layer called the epidermis (Fig. 9·3). It is not

perforated by stomata. The cortex is composed of many layers of thin walled cells that store abundant starch (Fig. 9·4). The cells are

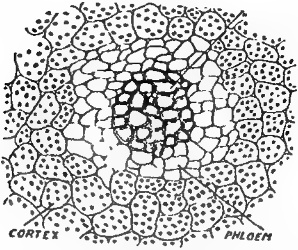

Fig. 9·4. T.S portion of Rhizome of *O. lusitanicum* cut from base. It shows a protostelic stelar organisation. Note the absence of endodermis and the presence of starch grains in the corticul cells.
(After Gewirtz and Fahn, 1960)

mostly oval or ellipsoidal in outline and enclose small intercellular spaces. The older parts of the rhizome in some species reveal the

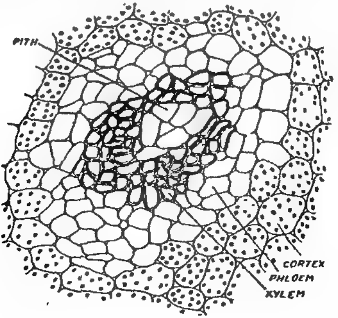

Fig. 9·5. T.S. portion of rhizome of *O. lusitanicum* cut from a place a little above the base. It shows a medullated protostele.
(After Gewirtz and Fahn, 1960)

presence of periderm which is not referable in origin to any cork cambium. Endodermis and pericycle are absent in majority of

species. Vasishta (1927) reported the presence of a distinct outer endodermis in the basal portions of the rhizomes in *O. aitchisoni* and *O. vulgatum*. Petry (1910) reported it in *O. pendulum*. Both outer and inner endodermis layers have been observed in the first formed portions of the stem in a species of *Ophioglossum* from Ceylon (Lang, 1912). The later formed or mature regions of the rhizome totally lack an endodermal layer.

Stele. In *Ophioglossum vulgatum* and *O. lusitanicum* the young rhizome reveals a protostele. There is a central xylem patch surounded by two to four layers of xylem parenchyma, a single layer of phloem elements and a definite endodermis which is present in *O. vulgatum* and absent in *O. lusitanicum*. The endodermis possesses distinct casparian strips. In the mature rhizomes the same structure (protostele) is shown by the basal portion (first formed) of the rhizome. A little above, the protostele becomes medullated, *i.e.*, a pith appears in the centre (Fig. 9·5). This is also called **ectophloic siphonostele.** At this stage the stele in *O. vulgatum*, consists of an outer endodermis, a single layer of phloem, xylem and a central pith. The endodermis, in this region of the rhizome, is considered to be an extension of the root endodermis. The continuity of the stele is not broken at this stage, by the gaps. Sections cut a little above the basal part reveal the absence of endodermis and perforation of the siphonostele by one or more leaf gaps. This perforated ectophloic siphonostele is called the **ectophloic solenostele.** There are two unequal bundles. The larger one is semicircular and the smaller may be oval or ellipsoidal in shape. Each one of them has phloem facing the epidermis and the xylem facing the pith (Colateral). The xylem is **endarch.** Higher up the ectopholic solenostele changes to a dictyostele (Fig. 9·3) due to the appearance of overlapping leaf gaps. The individual bundles composing a **dictyostele** are called the **meristeles.** Gewirtz and Fahn (1900) studied the vasculature of *O. lusitanicum* (Fig. 9·6) and revealed the same sequence of prototele, siphonostele, ectophloic solenostele and dictyostele from below upwards. They also reported that pith is intrastelar in origin. The mature rhizomes of *O. reticulatum* and *O. aitchisoni* also reveal the same variations in their stelar organisa-

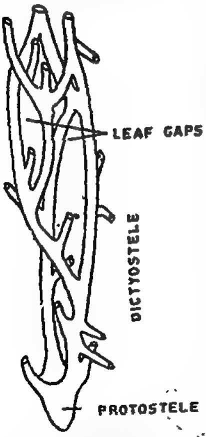

Fig. 9.6. Stereo-diagram of stele of *O. lusitanicum*. (After Gewirtz and Fahn)

tions from base upwards. In the latter species two leaf traces depart from a leaf gap (Vasishta, 1927). In this respect it resembles *O. palmatum*, *O. pendulum* and *O. fibrosum* In *O. palmatum*, Bower (1911) reported that the basal portions of rhizome reveal a medullated protostele.

It is clear from the above account that ultimately the mature rhizome has a dictyostele composed of a few meristeles. Each meristele is characteristic in lacking an endodermal layer. It has an outer patch of phloem which does not surround the xylem on all sides. So the organisation of the meristele is colateral and not concentric. The phloem consists of a single layer of sieve elements in *O. aitchisonii* and *O. pendulum*. In other species it may be four or five layers thick. Next to the phloem are a few layer of xylem parenchyma. Xylem faces the pith and is endarch. It is composed of tracheids. The metaxylem trachieds possess scalariform pits. The protoxylem shows variations in the lignification of its walls. Early formed protoxylem tracheids are usually annular. The rings of thickening material are joined to each other. Later the thickening pattern may change to reticulate type. In addition of reticulate thickenings, circular bordered pits may also be present in the mature protoxylem tracheids.

There is no secondary growth in *Ophioglossum*. The reported occurrence of little secondary growth in *O. vulgatum* (1899) has not been confirmed by any subsequent workers. Formation of isolated tracheids here and there in the pith has also been recorded in *O. aitchisonii* (Vasishta, 1927).

The pith is made up of starch filled, thin walled cells. The cells are smaller in size in the vicinity of the xylem elements and go on increasing in size towards the centre. Scattered tracheids have also been observed in the pith of *O. aitchisonii* (Vasishta, 1927) and *O. pendulum* (Petry, 1914). The occurrence of these is regarded by some as a sure evidence in favour of intrastelar origin of the pith.

Growing point [illegible] ical cell. [illegible] ows the ap [illegible] ere is a cavity which encloses the sunken apex, in the centre of which lies the apical cell. In longitudinal section the apical cell, in *O. aitchisonii* and *O. vulgatum* is approximately tetrahedral in form with four cutting faces and apex slightly truncate. According to Rostowzew the apical cell in *O. vulgatum* may be a three or four sided prism and the base may be truncate. The segmentation, as followed by Vasishta (1927) in *O. aitchisoni*, is regular along the three lateral sides. It is doubtful whether the segments on the basal side are so regularly cut off as on the three other sides. The large lateral segments retain their identity for a considerable time. The first divison in each segment is transverse. Thus the segment is divided into the lower smaller and the upper larger cell. The

lower cell divides again by a longitudinal wall into two. After that the divisions are irregular and difficult to follow.

B. The Leaf

(a) **Petiole** (Fig. 9·7). The petiole has a distinct epidermis composed of a single layer of slightly thick walled cells. The ground tissue of the petiole has a few layers of chlorenchymatous cells below the epidermis. The rest of it is made up of parenchymatous cells, that may enclose small intercellular spaces. The vascular bundles are embedded in the ground tissue.

The course of vascular bundles in the petiole of *O. vulgatum* is described below:—

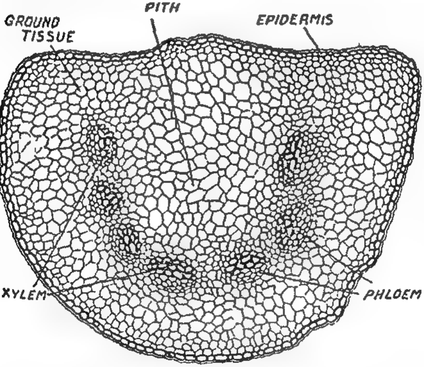

Fig. 9·7. T.S. petiole of *O. vulgatum*.

At the base of the petiole there is a single vascular bundle. It soon divides into three bundles which arrange themselves as the angles of a traingle. In the upper region of the petiole there are 5 to 7 bundles arranged in a semicircle in the sterile leaf. (*Fig.* 9·7). In the fertile leaf there are 7-10 bundles in the upper portion of the petiole. They are arranged in the form of a semi-circle or an ellipse. Three adaxial bundles go to form the vascular system of the spike, and the rest enter the lamina. Each vascular bundle of the petiole is more or less circular in outline. The xylem mass is flattened. The protoxylem elements are situated on the inner surface (*endarch*). The phloem is on the outer face and is separated from the xylem tracheids by xylem parenchyma. Thus the bundles are collateral and endarch. There is no distinct bundle sheath.

The leaf traces as they separate from the stem stele are collateral and endarch.

The young leaf grows by means of an apical cell. When young it is invested by means of a sheath developed from its base.

In O. *aitchisoni* there are two vascular bundles at the base of the petiole. Their xylem faces the adaxial surface. Both the bundles divide into four and as we go upwards the bundles divide repeatedly to form large number of vascular bundles in the upper region of the petiole. In the sterile leaves the bundles arrange themselves in the form of a 'U' open on the adaxial side In the fertile leaves the bundles in the upper part of the petiole, are arranged in a circle. At the base of the lamina they arrange themselve into two series, the inner and the outer The inner series, consisting of three or four bundles, constitutes the vascular system of spike. The outer series consisting of about 7-9 bundles forms the vascular system of the lamina, where they are arranged in a flattened arc.

(*b*) **Lamina** (Fig 9·8). The structure of the lamina is very simple. It consists of a distinct epidermal layer which is present on

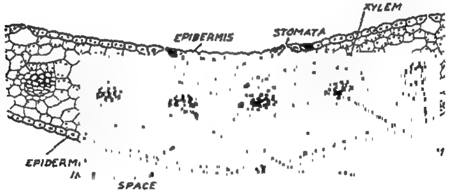

Fig. 9·8. V.S. lamina of *O. vulgatum*.

both the dorsal and the ventral surfaces of the leaf. On both the surfaces it is made of a single layer of more or less globular cells. The cells are rather thick walled. The epidermal layer is not continuous. Its continuity is interrupted at intervals by large stomata which are more numerous on the lower epidermis than on the upper epidermis in *O. aitchisoni* and *O. reticulatum*. In *O. vulgatum*

on both the epidermal layers

y other thick walled tissue.

palisade and spongy par-

d thin walled and

ot tissue or the **mesophyll**

which do not form any projections on the surface of the lamina.

monarch and diarch root stele in *O. berginanum* and Saxena and Mathur (1925) reported diarch root stele in *O. fibrosum*. Bower

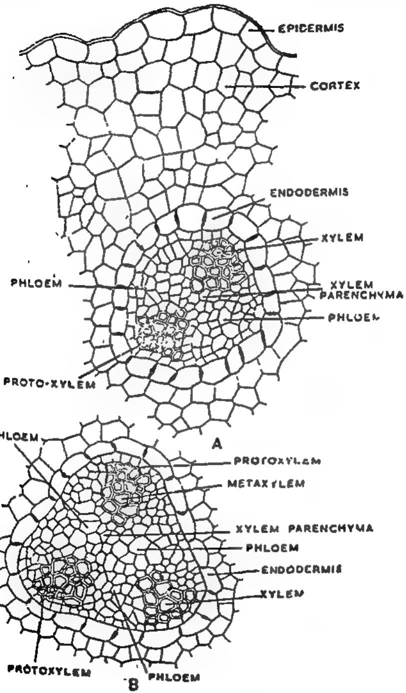

Fig. 9·10 (A—B). *O. aitchisoni*. A. T.S. portion of a diarch root. B. T.S. portion of a triarch root.

(1908) also found triarch stele in *O. decipiens*. Vasishta (1927) recorded diarch, triarch and tetrarch steles in *O. aitchisoni* (Fig. 9·10). He

observed that in *O. aitchisoni* there seems to be definite relationship between the size of the root and the presence of protoxylem groups. The strong roots have got triarch (Fig. 9·10, B) or tetrarch stele and delicate ones diarch (9 10, A). In *O. vulgatum* the stele is monarch (Fig. 9 9) and more or less saucer-shaped. The xylem mass in this species takes the form of an arc. On the curved side, it is separated from the endodermis by a single layer of xylem parenchyma, but sometimes a few tracheids abut directly on the endodermis The concavity is filled with parenchyma The phloem which is single layered except in the middle where it may be double, abuts directly on the endodermis and occupies the place opposite the xylem arc The roots lack secondary growth.

Growth of the root. The root grows by means of a tetrahedral apical cell. It cuts off segments on all the three sides, the outer of which forms the root cap. The root cap is not formed only from the outer segments, but cells are also contributed to it by the lateral segments. The divisions in the lateral segment, in *O. aitchisoni*, are irregular and the tissue here consists of very irregularly arranged cells. A little below the apex two regions can be distinguished, the central with narrow elongated cells called the **plerome** and the outer known as the **periblem**.

... cies of *Ophioglossum* reprod ... ititious buds on the roots. ... in *O. aitchisoni* and *O. vulgatum* Later Wardlaw (1953) induced their formation and development under natural and experimental conditions, in *O. vul-* ... ls on the entire and de- ... ty of such buds develop ... ition of such shoot buds ... developmental changes (Fig. 9·11, A—C):

(*i*) A group of parenchymatous cells in the root cortex start dividing. One or two such meristematic cells divide repeatedly to form a spherical or ellipsoidal mass of meristematic cells.

(*ii*) A few cells within this mass of meristematic cells elongate and divide longitudinally and form a nascent shoot apex.

(*iii*) The cells overlying the nascent shoot apex undergo lysis leading to the formation of an air space.

(*iv*) Appearance of first root and first leaf primordia in the developing shoot bud.

(*v*) Basipetalous development of an incipient vascular strand by the longitudinal division of the parenchymatous cells lying below the bud.

Goebel (1902 ... are modi- fied lateral roots ... according to Ward ...

Peterson and Cutter (1967) have demonstrated that decapitated roots of *O. petiolatum* bear larger number of adventitious shoot buds.

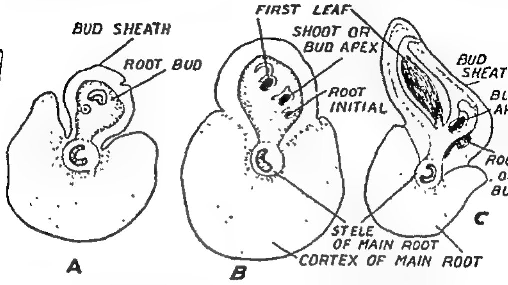

Fig. 9·11: *O. vulgatum*. Diagrammatic representations of cross-sections through the rhizomes of *O. vulgatum* showing the formation of adventitious buds (After Wardlaw)

Rostowzew (1891) noted the appearance of lateral buds on the rhizom of *O. vulgatum*. Such buds are of rare occurrence under natural conditions. Later (1953) Wardlaw induced the formation of buds on the decapitated shoots of *O. vulgatum*. They have an endogenous origin either from the pith or the cortex. Such buds grow into new plants and are therefore a means of vegetative propagation.

REPRODUCTION

The fertile spike The spike is a specialised ... leaf. The mature spike ... the stalk or the peduncle ... lamina of the sterile leaf ... the spike is broader and ... either side. The tip of ... conical in shape (Fig. 9 1...) The spike varies in length in various species. In *O. aitchisoni* (Fig. 9 1, A), *O. vulgatum* ... C) ... onger ... nd *O* ...

a ... characteristic in lacking
te ... long and cylindrical and

The sporangia free tip of the spike consists of parenchyma and contributes to the growth in length of iginate during the early ontogeny of the spike when it is very small in size. Its further growth and elon-

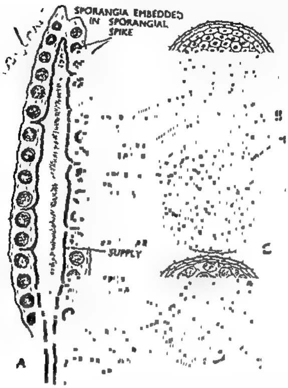

Fig. 9·12. *Ophioglossum vulgatum.*
A. Diagrammatic V.S. through a young spike showing sporangia free tip, the sporangia, the peduncle and the vascular supply.
B—D. Diagrammatic cross sections at various levels of the spike.

gation is not due to the activity of any apical cell. Peterson and Elizabeth Cutter (1967) attribute the growth in length of the spike due to an intercalary meristem present below the sporangial area. They removed the sporangia free tip of the spike and found that it did not effect the growth of the stalk or the peduncle

The pec ... in the sporangial region as a central a ... and conical tip. The sporangi ... udinal rows on either side of ... are completely embedded in ... is indicated by ... furrows alternate ... rom the ... during ... ter the sterile mass between the sporangia (Fig. 9·12). These lateral strands then bend towards the bases of the sporangia and constitute their

vascular supply. The number of sporangia embedded in each spike varies from six to twenty or even more.

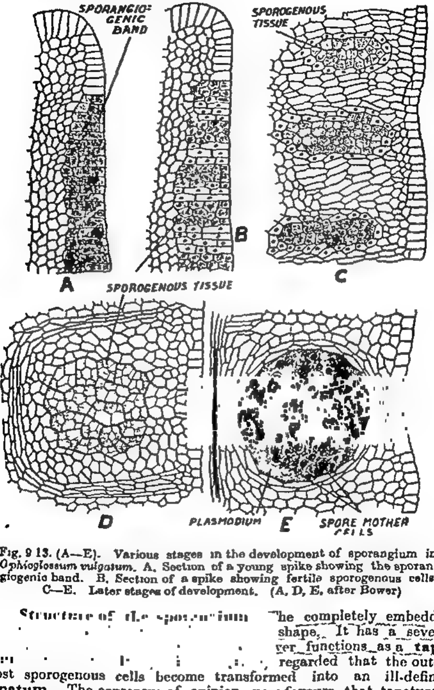

Fig. 9 13. (A—E). Various stages in the development of sporangium in *Ophioglossum vulgatum*. A. Section of a young spike showing the sporangiogenic band. B. Section of a spike showing fertile sporogenous cells. C—E. Later stages of development. (A, D, E, after Bower)

Structure of the sporangium The completely embedded ... shape. It has a several ... ver functions as a **tapetum** ... regarded that the outermost sporogenous cells become transformed into an ill-defined **tapetum.** The consensus of opinion now favours that tapetum is derived from the innermost wall lay... ium is filled with a compact mass o... **mother cells** (Fig. 9-13, D). The ... cytoplasm forms a continuous mass...

several tapetal nuclei embedded in it (Fig. 9·13, E). These free nuclei have been reported to increase ... 1908). The plasmodium serv ... dium penetrates in between ... isolated into larger and smaller blocks of cells (Fig. 9·14, A, B), which ultimately separate into individual cells and round off. They increase

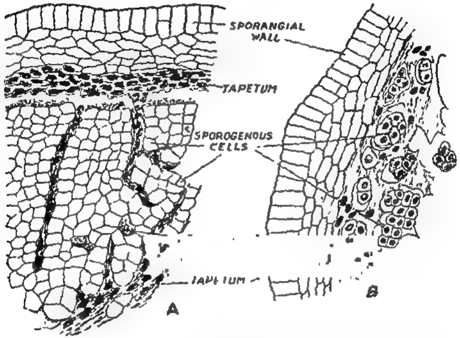

Fig. 9·14. Section through mature sporangia of *O. vulgatum* showing penetration of plasmodium in between the spore mother cells thus breaking them into larger (A) and smaller groups or blocks (B). (After Bower)

in size and undergo tetrad division to form tetrads of spores (Fig. (9·12, D). Usually all the spore mother cells are functional and form spore tetrads but in some larger sporangia some of the spore mother cells may degenerate. In the mature sporangium the wall consists of 3 – 6 layers of cells (Fig. 9·14, A, B). The cells of the outermost layer are radially elongated and larger in size. There are numerous spores within. The number of spores may reach 15,000 per sporangium in *O. pendulum* (Bower, 1935). The sporangial wall shows no distinction into an annulus and a stomium. All the cells are alike. Stomata have also been reported in the sporangial wall.

Dehiscence

... in the sporangial wall ... of sporan ... the ... al wall and gia ... terile tissue causes its dehiscence. The shrinking of the mass ... in the spike may cause the dehiscence of the sporangium. After the maturation of the spores the sterile cells of the spike lose water

and shrink and set up a strain that causes some weaker cells of sporangial wall to separate and form a transverse slit.

Development of the spike and sporangia (Figs. 9·13 and 9·14). Bo...
in *Ophiogl*...
outgrowth...
base of the...
apical cell...
... leads to the forma-
... rallel to the surface of the sterile lamina and the other two in a plane perpendicular to it. Further growth and division of the segments of the apical cell lead to the formation of a mound of tissue with a well defined epidermal layer. The epidermal layer formed along the two quadrants that are oriented parallel to the surface of the leaf lamina shows differentiation of its cells into two vertical strips of cells. These strips are called the **sporangiogenic bands** (Bower, 1896) and are several cells in height and two to three cells in the breadth. The sporangiogenic band does not extend throughout the length of the young spike. It occupies only the portion which is destined to bear the sporangia. The apex of the spike and its basal portions remain sterile. The latter forms the peduncle.

The cells of ...
So the two bands ...
cell of the spor...
that the band bec...
divide anticlinally ..
The inner cells, ...
divide in more than one plane and form groups of isolated cell called the **archesporial cells** (Fig. 9·13, B, C). Their cytoplasmic contents are denser and they prossess big nuclei and stain darker than other cells. Like this alternate bands of sterile and archesporial cells becomes distinguished in the hypodermal region of each sporangiogenic band (Fig. 9·13, B, C). The positions of groups of archesporial cells mark the positions of future sporangia. The cells of the sporangiogenic band external to each archesporial group divide periclinally and anticlinally and contribute to the portion of sporangial wall. The archesporial cells divide repeatedly to form a larger group ... he cells of the spike
... ne sporangial wall.
... y the sporangiogenic
band) and complete the spor...
of the sporangia are derived ...
partly from ...

... which undergo meiosis
... (Fig. 9·12, D).

Morphological nature of the spike. The following views have been expressed by various authors to explain the morphological nature of the spike in *Ophioglossum*.

1. Bower (1896, 1908, 1935) suggested that the simple spike of *Ophioglossum* originated as a result of condensation and lateral concrescence of the branched spikes of genera like *Botrychium*. He believed that the sporangia of the fertile spike are actually synangia derived by the partition or "fission" of the continous sporangia. He believed the two marginal rows of sporangia to be two continuuous sporangia which have become partitioned to form two rows of sporangia. Such an assumption is not supported by the course of vascular supply from the petiole to the sporangia. Bower later (1926) adandoned his own hypothesis and agreed to a greater extent with Zimmermann (1930) in considering the spike to be a fertile lobe of the leaf.

2. Roeper (1859) considered the leaf of *Ophioglossum* to be derived from a compound leaf whose two basal pinnae or leaflets became laterally fused to form the spike ... [illegible] (1926).

3. Zimmermann (1930) suggested that the fertile spike and the sterile lamina are the two dichotomies of a shoot. The former is meant for reproduction and the latter for photosynthetic functions.

The vascular supply from the petiole to the spike and the sterile leaf blade, no doubt, suggest that the spike is a modified segment of the leaf. A noteworthy feature in this connection is the growth of the spike. *After the* inception of the sporangiferous region the spike ceases to grow by means of an apical cell. It seems to elongate by the activity of an intercalary *meristem* (Peterson and Cutter, 1967) situated at the base of the *sporangiferous* region.

GAMETOPHYTIC GENERATION Homospore

The spore is a pioneer structure of the gametophytic generation. *Ophioglossum* is homosporous and the spores germinate to give rise to bisexual prothalli or the gametophytes.

The spores. They are produced in large numbers and are visible as small, yellow, dust like particles. They are tetrahedral in shape and possess a two *layered thick* wall. The outer wall is called the **exine** or the **exosporium** and is slightly thick and sculptured. The inner wall is thin and delicate and is called the [illegible] toplasm is granular and stores [illegible] s. The nucleus is centrally [illegible] but they lose this colour at maturity.

Germination of the spore (Fig. *9·15, A—C*). The germination of spores of some species of *Ophioglossum* has been *studied* under experimental conditions. The full details of germination *leading* to the formation of a mature prothallus are lacking. The *time* taken by the spores to germinate varies from a few days to a *few* months or even a year or two. Campbell (1907, 1911) studied *the* earlier stages of spore germination in *O. pendulum* (*Fig.* 9·15, A—C).

He observed that the spores of *O. pendulum* took 1½ years to germinate. ... ater and swell. The exine ... spore contents enclosed wi ... e slightly from ruptured ex ... equal cells by a transverse wall (Fig. 9·15, A). The cell below the triradiate mark is the upper cell. ... text by a vertical wall (Fig. 9·1 ... e young prothallus is now three ... three-celled stage have not been properly studied. Thirteen-celled ... his cultures but the ... or anything is known ... this stage. After the ... served mostly in the ... occasionally. Campbell ... gus enters the young ... 15, C). The entry is

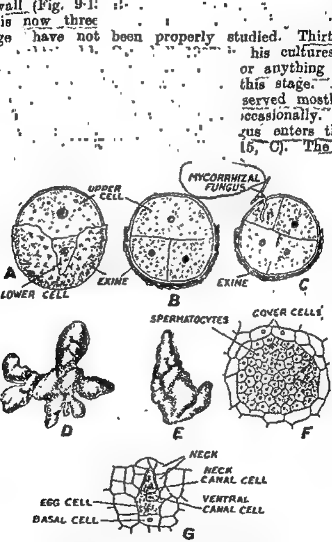

Fig. 9·15 (A—E). *Ophioglossum pendulum*.
A—C. Early stages of spore germination.
A. Two-celled stage. B. Three-celled stage. C. Four-celled stage.
Also note the ... of
of
m

effected through the lower cell. The thirteen-celled gametophytes of *O. pendulum* were more or less spherical or globose in shape and

did not bear rhizoids. Lang (1902) collected the prothalli of *O. pendulum*. She found that the young prothalli were almost spherical in shape and unbranched. The older prothalli were, however, much branched (Fig. 9·15, D). Smith (1955) collected mature prothalli of the same species and found them to be unbranched and more or less cylindrical in shape (Fig. 9·15, E). Lang (1902) described the branches of her specimens to be cylindrical and observed them to grow from a single four-sided and pyramidal intial cell. The mature prothalli of this epiphytic species were fixed to the substratum by means of numerous rhizoids. The endophytic fungus was restricted to the lower portion of the prothallus

Structure of the mature prothallus. The prothalli of O. [illegible] by hyaline, brownish, light [illegible]

[illegible] to [illegible]

prothalli in most species are perennial, but in *O. moluccanum* they are annual. The shape of the prothallus also varies. It may be roughly cylindrical or sometimes irregularly lobed and in some cases conical. The prothallus in the common *O. vulgatum* is more or less cylindrical (Fig. 9.16, A, I [illegible] but branched and massive prothall [illegible] by Bruchmann (Fig 9·16, B). The I [illegible] is massive and almost bulbus and [illegible] part arises an upright and cylindrical region that grows straight by means of a tetrahedral apical cell. *This region* may bear adventitious branches (Fig. 9·16, B). The apical region of the upright cylindrical [illegible] It is also absent in t [illegible] A). The endop [illegible] ls in the lower [illegible] The [illegible] internal cellular differentiation [illegible] y elongated and filled with [illegible] all over the upright [illegible] have [illegible] over [illegible] are

[illegible] which he

[illegible]

The branches are oriented in three dimensions. [illegible] free and portions of the prothallus die leaving the number of branches [illegible] branch grows into a fullfledged prothallus. [illegible] prothallus by fragmentation. [illegible] igus. Unicellular and papilla [illegible] species.

Pant and Misra (1973) have studied in detail the gametophytes of six Indian species (*O. vulgatum*, [illegible] *costatum* and *O. gramineum*. [illegible] drical and in to some cases br[illegible]

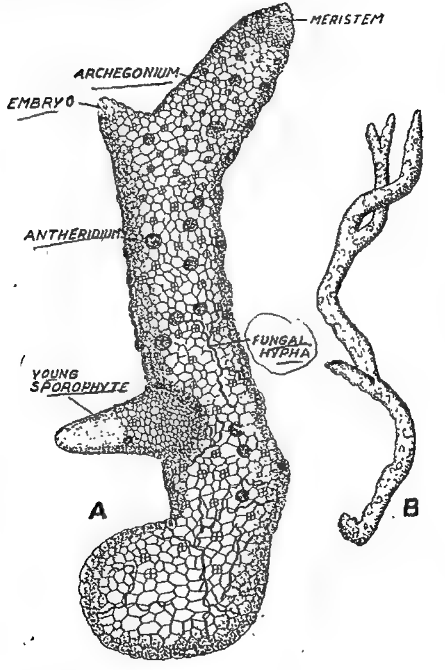

Fig. 9·16 (A—B). *Ophioglossum vulgatum.*

A. A mature gametophyte bearing sex organ. A young sporophyte is also seen on one side.

B. The same as A, showing branching. (After Bruchmann)

may project above soil and turn green. They did not observe stomata but found rhizoids in all the species. Some prothalli were monoecious whereas others were dioecious. In all of them sex organs develop acropetally from superficial initials.

Sex organs. [illegible] found on the [illegible] gled (Fig. [illegible] and arise [illegible] respect to each other and it is not surprising to come across the gametophytes in which either type of sex organ predominates the other in numbers. Dioecious prothalli have not been recorded under natural conditions in *Ophioglossum*. The structure and development of antheridia and archegonia is described below.

Antheridium

(a) **Structure** (Fig. 9·17, F). The antheridia are generally comp[illegible] may be slightly projectir[illegible] less ovoid in shape at m[illegible] rived from the wall initial and partly from the surrounding prothallial tissue. It is one layer of cells in thickness. Nozu (1961) described a two-layered thick wall in *O. vulgatum*. Such a condition is not common. The [illegible] f androcytes which later metamor[illegible] number of spermatozoids in each [illegible] housands. A triangular cap cell or opercular cell is visible in the antheridial wall when viewed from [illegible] the dehisc[illegible] cular cell [illegible]

[illegible] 9·17, G) and those [illegible] known among the [illegible] and coiled region [illegible] e blepharoplast and [illegible] and loosely coiled. It is nuclear in origin. A distinct vesicle is also discernible at the posterior region.

(b) **Development** (Fig. 9·17, A—E). A superficial cell of the prothallus, a little distance behind the apex, functions as the antheridial initial. It divides by a periclinal wall into an outer cell called primary cover cell [illegible] primary wall cell. The outer cell gives [illegible] wall and an opercular cell. The [illegible] androgonial cells.

The outer cell divides into two equal cells by means of an anticlinal wall. A second wall is laid down in such a manner so as to establish a triangular apical cell with three cutting faces (Fig. 9·17, D). This cell is capable of dividing along its three faces. The segments thus cut off form a portion of the antheridial wall. This triangular cell, after stopping to divide, functions as the opercular cell. The rest of the antheridial jacket is derived from the surrounding prothallial cells.

The inner cell divides by transverse and vertical walls to form a quadrant of androgonial cells. These cells divide further by vertical walls and then by both vertical and transverse walls to form a large number of androgonial cells that divide further to form several thousand **androcyte mother cells.** The androcyte mother cells divide once to form **androcytes.** The protoplast of each androcyte metamorphoses into a single multiflagellate antherozoid.

Each androcyte mother cell has two blepharoplast granules, one on either side of its nucleus. The resulting two androcytes have a blepharoplast each. During the metamorphoses of the spermatozoid, the blepharoplast elongates into a coiled thread-like structure that touches the nucleus at one end. The nucleus also becomes loosely coiled and forms the posterior portion of the spermatozoid. The coiled blepharoplast forms the anterior end of the spermatozoid and bears numerous flagella. The unused cytoplasm forms a small vesicle at the posterior end.

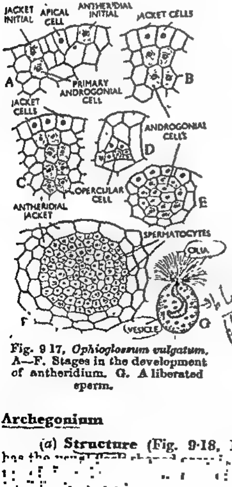

Fig. 9.17, *Ophioglossum vulgatum.* A—F. Stages in the development of antheridium. G. A liberated sperm.

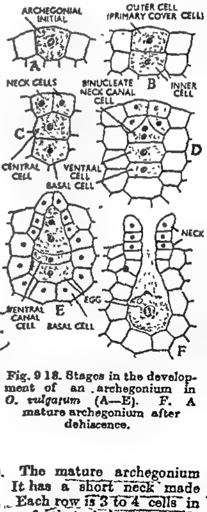

Fig. 9.18. Stages in the development of an archegonium in *O. vulgatum* (A—E). F. A mature archegonium after dehiscence.

Archegonium

(*a*) **Structure** (Fig. 9.18, E—F). The mature archegonium has the usual flask-shaped ... It has a short neck made ... Each row is 3 to 4 cells in ... neck canal that lodges a single

binucleate **neck canal cell**. Sometimes the two nuclei are separated by a cell wall thus leading to two uninucleate neck canal cells. The venter consists of a single **ventral canal cell**, which ... cell ...

cell disorganise in a mature archegonium. The neck cells at the top also separate thus making an open channel for the sperms to enter (Fig. 9·18, F).

(*b*) **Development** (Fig. 9·18 ... is also a superficial cell of the prot... and an inner cell by a pericli... **primary neck cell** or the **prim... cover cell** ... divides by a periclinal wall into a ... central cell ... the primary neck cell) and a low... cell divides by two intersecting ... rately arranged **neck-cells**. The cells by further transverse divisions give rise to four longitudinal rows of neck cells, each row having 3 to 4 cells Meanwhile the central cell divides into an outer **primary neck canal cell** and an inner **primary venter cell**. The former enlarges in size and pushes in between the neck cells. Its nucleus divides into two daughter nuclei forming a binucleate neck canal cell. The primary ventral cell divides into an upper **ventral canal cell** and a lower **egg cell**. The ventral canal cell is ephimeral and short-lived. It soon degenerates. The **basal cell** does not divide further. Nozu (1961) observed that in *O. vulgatum* the two nuclei of the neck canal cell become separated by a wall, thus forming two uninucleate neck canal cells.

The process of fertilisation has not been observed in any species of *Ophioglossum*.

EMBRYOGENY

The fusion of the spermatozoid nucleus and egg nucleus re-establish a diploid nucleus or the synkaryon. The cytoplasm of the fertilised egg clothes itself with a wall and is now called a **zygote** or the **oospore**. The oospore is the pioneer structure of the sporophytic generation.

Campbell (1911, 1940) reviewed the embryogeny of the genus *Ophioglossum* and recognised the following three types :

1. *Ophioglossum vulgatum* type as described by Bruchmann in 1904 (Fig. 9.19, A—E).

2. *O. moluccanum* type as described by Mettenius in 1856.

3. *O. pendulum* type as described by Lang in 1902 and by Campbell in 1911, 1921 and 1940.

... O. ... (1904) gave a det... After fert... like

by a transverse .m (Fig. 9·19, A) epibasal and a hypobasal cell. ormed and the

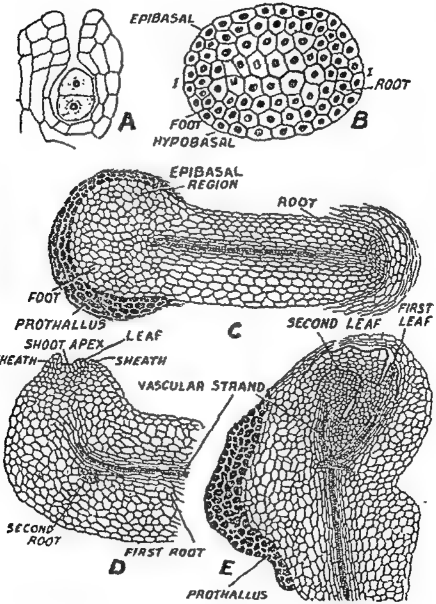

Fig. 9·19 (A—E). *Ophioglossum vulgatum.* Stages in the development of embryo.

A. L.S archegonium showing the first division of the zygote;
B. Post-octant stage of embryo;
C. L.S older embryo showing well developed first root;
D. L.S of mature embryo showing shoot apex and first leaf;
E. L.S. older embryo showing shoot apex and first two leaves;

(After Bruchmann)

embryo [illegible] exoscopic [illegible] the shoot and the [illegible] ot and the root. [illegible] observed. The ne[illegible] oval mass of cells as visible in a median section. The first wall (1—1) is indicated and it is clearly shown that both the foot and the root develop from the hypobasal region (Fig. 9·19). The epibasal part remains an undifferentiated mass of meristematic cells for a considerable leng[illegible] root [illegible] of the [illegible] root is [illegible] kwards to the region [illegible] e root remains small and does not undergo any massive development. This [illegible]

[illegible] elongated cell between the first leaf and root strand represent the incipient vascular strand of the first leaf. Later it becomes joined with root strand. Similarly a second leaf along with leaf sheath makes its appearance in the apical region (Fig. 9.19, E). It also develops its vascular strand that cojoins the vascular strand of the root. Meanwhile the apex of the second root also becomes organised (Fig. 9 19, D). The first leaf cannot grow beyond a certain height and remains below ground. It is the second leaf [illegible] nd comes above ground as the first [illegible] bears no spike. Development up to [illegible] me. The third leaf that appears in the next season may be fertile and may bear a spike. The shoot apex is very slow growing and appears as a small bud at this stage. The young sporophyte at this stage has three or four unbranched roots. Bruchmann also observed a small adventitious bud on one of the roots.

For variations in embryo development in other species please see chapter 8 (Early embryology in Eusporangiate Ferns).

Chromosome number. The number of chromosomes has been ascertained in a number of species. Abraham and Ninan (1954) counted $2n=1,260$ in *O. reticulatum*. In *O. petiolatum* the diploid number is about 1,000. The [illegible] *O. lusitanicum* it ranges [illegible] oth uni- [illegible] *He also* [illegible] *to the* [illegible] Ninan [illegible] *m to be* [illegible] on. The [illegible] l closed [illegible] strands [illegible]

CHAPTER X

PROTOLEPTOSPORANGIOPSIDA

The class Protoleptosporangiopsida is an assemblage of interesting ferns. The class includes both living and fossil members all of which are included in a single family Osmundaceae which is placed under the order Osmundales. The members of this class can be regarded as intermediate between the Eusporangiopsida and the Leptosporangiopsida, but they should in no case be regarded as phylogenetic links between them. They have a long evolutionary history and were represented in the Permian by such fossil genera as *Zalesskya* and *Thamnopteris*. The living members of this class can be regarded as the 'living fossils'. The living Osmundales resemble the Eusporangiate ferns in the following respect :

1. Eusporangiate, development of the sporangium.

2. The sporangia are massive and produce larger number of spores. The sporangia are not arranged in distinct sori.

3. The structure and development of the archegonium.

4. The antheridia are larger in size and have many wall cells and produce many spermatozoids.

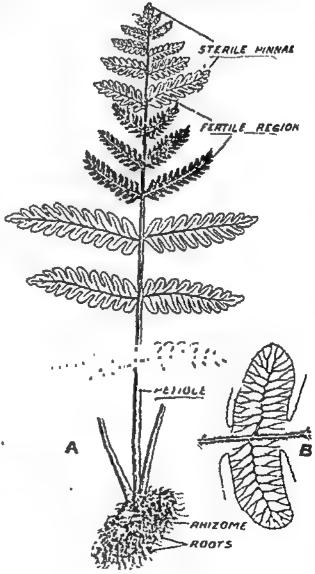

Fig. 10-1. *Osmunda claytoniana.* A complete plant showing habit.

5. The prothallus is thick and massive and long lived like that of *Marattia*.

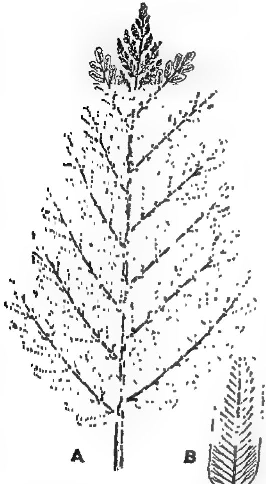

Fig. 10 2 *Osmunda regalis*.
A. Portion of a frond bearing sterile and fertile pinnae. The fertile region is terminal.
B. A pinnule showing venation.

6. Internal structure of the petiole. The endodermis is not very distinct and there are also present mucilage canals near the vascular bundle. In this respect they resemble the marattiales.

7. Presence of stipule like expansions at the base of the petiole. They resemble the leptosporangiate ferns in the following characteristics:

1. Origin of tapetum from the archesporial cells.

2. Presence of a primitive type of annulus in the sporangia.

3. The wall of the sporangium is single layered.

4. The antheridia and archegonia are of projecting type.

5. The prothallus lacks an endophytic fungus and is of cordate type.

6. Embryo development is of prone type, i.e., the first division of zygote is vertical.

The class as a whole exhibits the following characteristics:

1. The members of this class are terrestrial and possess thick, hard and upright rhizomes that may attain large diameters. The rhizomes do not possess any scales.

2. The leaves are large and pinnately compound. They may be unipinnate, bipinnate or multipinnate. The expanded leaf bases are covered with glandular hair. The venation is of open dichotomous type.

3. The young leaves are circinately coiled and are covered with hair.

4. The leaf bases are persistent and become sclerenchymatous. They give an added mechanical strength to the rhizome and increase its diameter.

5. The stelar organisation in the stem is dictyoxylic. The internal endodermis is present in *O. cinnamomea*. In *Todea* internal phloem is present but internal endodermis is absent. The xylem elements resemble those of the marattiales.

6. The stem stele is surrounded by numerous steles of the persistent leaf bases.

7. The sporangia bearing leaflets are quite different from the sterile leaflets. They are much reduced in *Osmunda*. The sporangia do not form

sori and are scattered and superficial. All of them mature simultaneously. In *Osmunda* they are marginal in position. Indusium is absent.

8. The sporangia are short stalked and massive, globose structures, with a larger spore output. They have a terminal annulus. Dehiscence takes place by means of a slit running from the annulus along the upper face of the sporangium to its ventral side.

9. The spores are tetrahedral and green in colour and lack a perispore.

10. The prothallus is epiterranean, green cordate, long lived and tuberous structure. It has no mycorrhizic fungus The prothallus is prominently thickened in the midrib region. The prothallus is usually monoecious but unisexual prothalli are not rare.

11. The sex organs are of emergent type. The archegonia have six tiers of neck cells and are produced along the margins of the swollen midrib. The antheridia develop along the margins of the prothallus. In unisexual and slender prothalli the antheridia may develop terminally on small branches (*O. claytoniana*). The development of the antheridium neither resembles eusporangiate type nor it resembles the leptosporangiate type.

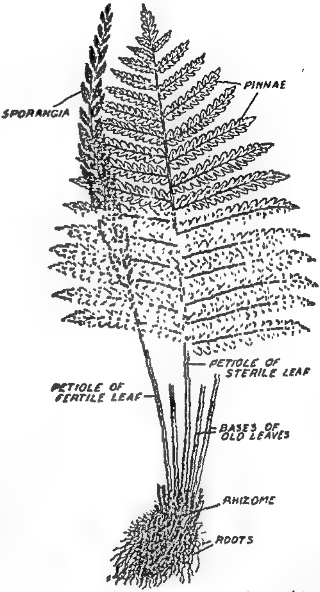

Fig 10 3. *Osmunda cinnamomea*. A complete plant bearing sterile and fertile fronds.

12. The development of the embryo is neither exoscopic nor endoscopic. The zygote divides first by a vertical wall and again by a second vertical wall. The third wall is transverse

Hirmer (1936) named this class as **Protoleptosporangiata.** Reimer (1934) and Pichi-Sermolli (1959) named it as **Osmundidae.** The class includes a single order **Osmundales** which includes the family **Osmundaceae** The family includes three living genera (*Osmunda*, *Todea* and *Leptopteris*) and about three fossil genera (*Zalesskya*, *Thamnopteris* and *Osmundites*). The genus *Osmunda* is described as a type in this text. *Todea* is a monotypic genus and is represented by *T. barbara* which is

met with in Australia, New Zealand and South Africa. *Leptopteris* [redacted] represented by six species that are restricted to New Zealand and Polynesia. It is characterised by thin leaves that lack stomata.

OSMUNDA L.

It [redacted] widely distributed genus and is found in both tropical and temperate regions of the world. It
(Christensen, 1938). Smith mentic
to this genus. In India it is repres
O. claytoniana and *O. cinnamome*
very common at higher altitudes in
10,000 feet. It grows at a height of 3,000 metres or even more in the Simla Hills (Huttoo Peak). *O. regalis* also grows in Simla Hills at an altitude of 1,500 metres at a place known as Chadwick falls. The plants growing here are usually sterile. They seem to prefer shaded and cool localities and are very much restricted in distribution. They occur in isolated patches. The plants of *O. claytoniana* (Fig. 10 1) growing at Kedar Nath bear abundant sporangia during the months of June and July.

External Features. All the species of *Osmunda* are medium sized ferns, … height of two to thr… and upright in … and stumpy str… is dichotomou… may … with the bases of … They give … close spirals …

way out. The roots are hard, rough to touch and black or dark brown in colour. They are profusely branched and bear brown root hair just below their tips. The rhizomes with their leaf bases and tufts of roots may reach a diameter of a foot or so.

… coiled when young. An unfolded … (*O. claytoniana*) … of *O. cinna-* … of two to three … to form stipule … ons are covered … for one season … ve their persis- … of the petiole … e young leaves

they are herbaceous (*O. claytoniana*). The leaflets of the lamina are

usually leathery in texture and may be entirely or variously incised. The unipinnate leaves of *O. claytoniana* are im-paripinnate. The number of pinnules in the bipinnate leaves of *O. regalis* is also odd. T' [illegible] and they gradually go on becom- [illegible] l of the lamina so as to give it a [illegible] e (Fig. 10·2). The young and [illegible] with unbranched multicellular hair which fall off as the leaf matures. The leaves are arranged in close spirals and form a 'basket-shaped' crown at the summit of the rhizome.

The leaves may be monomorphic (*O. regalis*, *O. claytoniana*) or dimorphic (*O. cinnamomea*, *O. japonica*). In *O. cinnamomea* two types of leaves appear on the stem. These are the sterile leaves which appear late in the seaso[illegible] earlier (Fig. 10·3). The fertili le [illegible]

[illegible] in the same leaf [illegible]

mal pinnae are sterile (Fig. 10 1). In *O. regalis* (Fig. 10·2) the fertile region is terminal. *O. vachellii* is an example where the pinnae at the base of the leaf are fertile. These fertile pinnae either lack green lamina or the latter is very much reduced. Caponetti, J.D. (1972) relates the occurrence of different types of leaves to the complement of soluble proteins and enzymes in the shoot apex and leaf sets of *O. cinnamomea*.

ANATOMY

Rhizome (*Figs.* 10·4 and 10 5). The rhizome grows by means of tetrahedral apical cell. A transverse section of the rhizome reveals the following arrangement of the tissue from outside within:

Cortex. It is distinguishable into two well defined regions: (*a*) the outer cortex and (*b*) the inner cortex. The outer cortex is composed of several layers of thick-walled cells. The boundary of the outer cortex is irregular due to the presence of persistent leaf bases. There is no definite layer of epidermis bounding it as all the cells are sclerenchymatous. The cells are all dead and black in colour. In this region lie embedded numerous spirally disposed leaf traces (Fig. 10·4). This region gives mechanical strength to the rhizome. The inner cortex is made up of a few layers of thin walled cells. The cells are filled with starch grains. Some leaf trace bundles are also present in this region (*Fig.* 10·4).

Each leaf trace bundle is C-shaped (Fig. 10·4) and consists of an outer endodermal layer followed by 2 to 3 layers of pericycle. The phloem comes next and surrounds completely the central xylem

strand. The xylem is horse-shoe shaped (Fig. 10·4). The proto xylem is situated on the concave side as a small mass of spirally

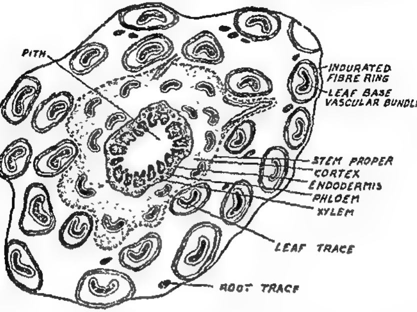

Fig. 9·4. T.S. (diagrammatic) of rhizome of *O. regalis*.

thickened tracheids. The rest of the xylem is made up of larger scalariform tracheids. The convex side of the xylem faces the periphery of the stem. The phloem consists of sieve tubes with sieve plates on their lateral walls.

Endodermis. Next to the inner cortex is the *endodermis.* The endodermal cells possess distinct casparian *bands (Fig. 10·5)* on their radial walls. In *O. cinnamomea*, Faul (1901) recorded the presence of an inner endodermis. Endodermis forms a complete boundary around the stelar region and runs uninterrupted. *It is*, no doubt, absent at places where there is a branch gap.

Pericycle. It forms 2—4 layers of parenchymatous cells next to the endodermis.

Stele. The stele consists of a varying number of C-shaped or horse shoe-shaped xylem bundles surrounded by a continuous *ring* of phloem elements (Fig. 10·5). The outer cells of phloem constitute the protophloem. The phloem is composed of distinct *sieve tubes* with sieve plates on their lateral walls. The phloem *cylinder is* thicker at places opposite the leaf gaps or the so-called *medullary* rays. The sieve tubes are characteristic in having their *long axis* tangential to that of the stele (Fig. 10·5). Zenetti (1893) *described* them as "quergestrecktetzellen". Faul (1901) regarded *them as* sieve tubes of the metaphloem. Next to the phloem sheath *is the* several layered xylem sheath which is made up of parenchyma cells (Fig. 10·5). It completely encircles the xylem strands. There is every possibility that it is composed of xylem parenchyma and phloem parenchyma cells.

The xylem appears in the form of discrete strands of variable shapes and sizes. Most of them are horse-shoe shaped, some are oval and others irregular in shape. These strands are separated by narrow parenchymatous bands that connect the central pith with the xylem sheath. These are the leaf gaps. Each xylem strand

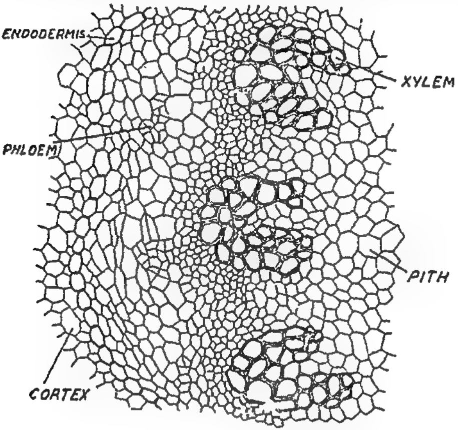

Fig. 10·5. T.S. portion of stelar region of O. claytoniana.

consists of scalariform metaxylem tracheids and annular and spiral protoxylem tracheids. The former are larger in diameter than the latter and constitute most of the xylem tissue. In the horse-shoe shaped strands the protoxylem forms a small group of tracheids lying in the concavity of the metaxylem (Fig. 10·5). In the oval or irregular strands the protoxylem is surrounded on all sides by the metaxylem (mesarch). The number of xylem strands may be as many as forty in *O. claytoniana* and about fifteen in *O. regalis*. Bierhorst (1960) recorded the presence of pits in the walls of metaxylem tracheids.

Faul (1901) reported the presence of both external and internal endodermis and phloem in *O. cinnamomea*.

Pith. It occupies the centre of the stem and is parenchymatous and quite conspicuous (Fig. 10·5). The pith is wholly parenchymatous in *O. claytoniana*. In *O. regalis* and *O. cinnamomea* a

few strands of sclerenchyma may be scattered in the pith. These may be regarded as tracheids.

The stele in *Osmunda* has been designated as a dictyostele by some workers. Sporne (1966) regards it as dictyoxylic. Due to the presence of continuous endodermis, pericycle and phloem layers external to the xylem, it does not fulfil the conditions met with in the dictyostele. The individual xylem strands can also not be regarded as meristeles. A meristele in its essentials has its own separate phloem, pericycle, and an endodermis. This condition is not obtained in any species of *Osmunda*. The stelar organisation in the younger and first formed parts of the rhizome is protostelic (Gwynne-Vaughan, 1911).

The Leaf

Petiole. A transverse section of the petiole reveals a distinct layer of epidermis, which in younger leaves is covered with numerous simple and multicellular hair. Next to the epidermis is a few layers thick sclerenchymatous hypodermis. The hypodermis encircles a broad central ground tissue. The ground tissue is composed of thin walled cells. In it is embedded a single petiolar bundle. The bundle is crescentic or horse-shoe shaped and has a central xylem core surrounded on all sides by phloem. Endodermis is not very clear. The xylem has several protoxylem groups along the concave side. The metaxylem consists of large tracheids that have scalariform thickenings. It makes up most of the xylem tissue. A number of mucilage canals are present towards concave side of the vascular bundle—a feature which it shares with the Marattiales.

Leaflet. A cross section of the leaflet reveals the presence of two epidermal layers. The stomata are present on the lower epidermis. In between the two epidermal layers is the undifferentiated mesophyll region. The cells of the mesophyll enclose intercellular spaces of variable dimensions. The cells contain chloroplasts and are the main seat of photosynthesis. They are compactly arranged below the upper epidermis and go on becoming loosely arranged towards the lower epidermis. The mesophyll cells are compactly arranged in the region of the midrib and the veins. There is a single vascular bundle in the midrib. It is concentric.

Root. The roots arise endogenously from the rhizome. There is a distinct outer layer or the epidermis in the young roots (Fig. 10·6). It is later replaced by the outermost layer of the cortex. It is called the exodermis. Next to the epidermis is a few layered hypodermis which is made up of thick walled cells. Its cells are smaller in diameter than those of the cortex. The rest of the cortex is parenchymatous. There is a distinct endodermis surrounding the central stele. The endodermis of the root is continuous with that of the rhizome and the petiole. Next to the endodermis are two layers of thin walled cells. These constitute the pericycle.

The stele is usually diarch but Faul (1901) reported triarch

stele in some species. There are tow xylem bundles that meet in the centre and appear as an elliptical central core of xylem. The protoxylem is exarch in position. It is represented by two groups on either side of the ellipsoidal xylem mass. There is no pith. Phloem forms two patches on either side of the xylem (Fig. 10 6). There are a few layers of thin walled cells between the xylem and the phloem bundles.

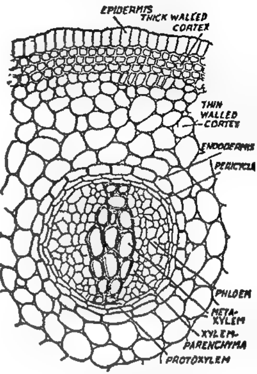

Fig. 10-6. T.S. part of root of *O. regalis* showing detailed internal structure.

The first or the primary roots in *Osmunda* grow by means of a single four sided apical cell. The adventitious roots, according to Bower (1889), may show a single apical cell in the beginning. Later it is replaced by a number of apical initials. Campbell (1911) described the presence of a single four-sided apical cell in *O. claytoniana* and *O. cinnamomea*. According to him the young segments cut off by these cells are larger and look like apical cells.

REPRODUCTION

... hin ... gia. ... lly ... ate. The fertile pinnules are restricted to the distal region of the leaf. In ... season are entirely fertile. ... uced. They have no sterile ... levelop on the veins arising ... ngia borne on these slender and thinned out leaflets give the appearance of lateral tassels of sporangia (Fig. 10 7). Pinnules with lower fertile region and upper sterile region are also met with (Fig. 10 8). In such case the lower proximal parts of the pinnae bear sporangial tassels whereas the distal sterile part has a well developed sterile lamina. In still other cases (Fig. 10-7) the fertile pinnules have well developed lamina with ... margins. In *O. claytoniana* ... or the pinnae are deeply ... nnules. The fertile pinnae in this species are restricted to the middle of the leaf (Fig 10-1). The sporangia are borne on the margins of the pinnules. The fertile

pinnae are bladeless and slender, with the result that pinnules also appear as short slender stalks with sporangia arising in clusters

So a sporangial tassel corresponds to a section of the sterile leaflet. In *O. cinnamomea* there are two kinds of leaves, the sterile ones

Fig. 10·7. *Osmunda regalis.* Portion of leaf bearing sterile, partly sterile and partly fertile and wholly fertile pinnules.

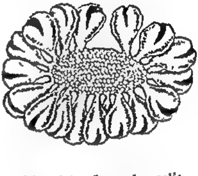

Fig. 10·8. *Osmunda regalis.* Transverse section of a tassel of sporangia. Note the arrangement of sporangia. (After Bower)

and the fertile ones. The fertile ones are reduced and bladeless (Fig. 10.3). The sporangia are naked, *i.e.*, they are not covered by indusia or scales or hair of any type.

An abnormal position of the sporangia was recorded in *O. claytoniana* (Chowdhry, 1932). Some of the sterile pinnae were seen to possess sporangia on their abaxial surface. The sporangia ... innae were found in the ... sterile pinnae.

SPORANGIA

Structure and Dehiscence (Fig. 10·9, E—H). A mature ... of *O. regalis* and most other species of *Osmunda* is a ... cture. The stalk is many ... ent species. The capsule ... Next to it there are two ... lls surrounding a central ... tapetal cells do not dis... fluid. In *O. claytoniana* ... The inner layer is derived ... disorganises to form the ... ate and push their way in between the spore ... ir walls disintegrate and their protoplasts fuse with each other to form a network like plasmodial fluid. It disappears during the maturation of spores. The

outer layer of tapetal cells is derived from the primary archesporial cell. It is made up of a single layer of flattened cells and persists

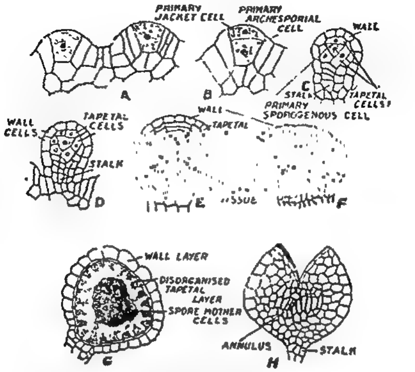

Fig. 10.9 (A—H). Stages in the development of sporangium. A—F. *O. regalis*. F. *A synangium of O. regalis*. G—H. *O. claytoniana*. (A—F, after Bower; G—H, after Smith)

throughout the life of the sporangium. It may be regarded as a functionless second wall layer. It plays no role in protection and dehiscence of the sporangium nor it nourishes the spores. The spore mother cells undergo meiosis and produce 128—512 spores.

The mature sporangium develops a transverse group of thick walled cells on one side (Fig. 10·9, H). This ... ulus. In some ... e of the ... breadth ... vertical ... presents ...). These ... slit ex-

Development ... e development of ... gia appear as sm... or their seg- me... gle sporangial ini... y large size, distinct ... ransverse wall ... and an inner

cell (Fig. 10·9, B). The former is called the **primary jacket cell** and the latter as **primary archesporial cell** (Fig. 10·10, B). The shape of the primary archesporial cell varies. It may be like an inverted pyramid with a truncated lower end or it may have a pointed lower end. *The former condition is considered to be prevalent in the eusporangiate sporangia and the latter in leptosporangiate types.* The archesporial cell cuts off three peripheral cells (Fig. 10·9, C) enclosing a **central primary sporogenous cell.** *The peripheral*

Bower. Their

in the leptospor

complete layer of tapetum internal to the wall layer (Fig. 10·9, D). *The tapetum may become two or even three-layered thick. This may happen by the periclinal division of the primary tapetal cells, or the second layer of tapetum is derived from the outermost cells of the sporogenous mass.* The latter condition is achieved in *O. claytoniana* (Smith, 1938). The primary sporogenous cell divides repeatedly to form 32—128 spore mother cells. The tapetal layers in *O. regalis* do not disorganise to form a plasmodial fluid. This condition reminds us of a similar state of affairs in the lycophyta. It has been regarded by some authors that the tapetal layer derived from the archesporial cell is in reality a second wall layer because

modial fluid. In *majority* of

is therefore regarded as a

be a sound reason for dis-

rs in the lycopodiales,

Moreover in *Osmun-*

not the wall become

e primary wall cells

rived from the outer-

, H) in a manner des-

The stalk of the sporangium is derived entirely or partially from the surrounding cells. The whole of the sporangium can, therefore, not be traced to a single cell. *The development is, therefore, essentially eusporangiate although* there is a trend towards leptosporangiate development. Bower (1935) reported a synangium formed by the partition of the sporangium into two sporogenous groups (Fig. 10·10, F).

The spore mother cells undergo meiosis to form 128-512 spores.

observed the haploid number of

GAMETOPHYTIC GENERATION

It starts with the spore whose structure and germination is described below.

Spore (Fig. 10·10, A). The spore is almost spherical in shape and possesses a distinct triradiate mark. The spore wall consists of the usual two layers. The outer variously sculptured exine and

an inner thin intine. In some cases a thin perispore is also present external to the exosporium. The perispore is formed by the deposited remains of the plasmodial fluid. The spore protoplast has a distinct centrally located nucleus (Fig. 10·10, B) surrounded by cytoplasm which contains numerous chloroplasts. The green spores of *Osmunda* remain viable approximately one week under field conditions (Lloyd and Klekowsky, 1970).

Germination of the spore (Fig. 10·10, C—H). Campbell (1892) studied the germination of spores in *O. claytoniana* and *O. cinnamomea*. Under [illegible]

[illegible] all **primary rhizoidal cell** [illegible] **prothallial cell.** The former comes out first in the form of a conical protuberance (Fig. 10 10, C) and the latter is still enclosed within the rupturing exine. The rhizoidal cell contains a few chloroplasts which later on, as it pushes its way down into the soil as a first rhizoid, disappear (Fig. 10·10, D, E). The larger [illegible]

[illegible] tion). There are some variations in the pattern of the laying down of first walls in the prothallial cell. In *O. claytoniana* (Campbell, 1892) the prothallial cell divides by a few transverse walls (Fig. 10·10, D) to form a filament of green cells. The terminal cell of the filament divides by two intersecting oblique walls (Fig. 10·10, F) to include a triangular apical cell with two cutting faces. The lower cells of the filament may now divide by longitudinal walls (Fig. 10 10, F). The apical cell cuts off segments towards its right and left in a regular, alternate manner. The segments cut off by the apical cell divide each by a transverse wall to form an outer and an inner cell.

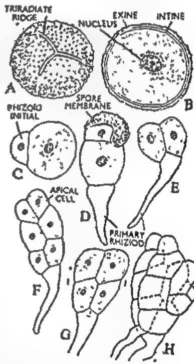

Fig. 10·10. Germination of the spore and early stage in the development of the prothallus in *Osmunda*: A—F. *O. claytoniana;* G—H. *O. cinnamomea.* (After Campbell)

The inner cells divide by horizontal walls. This adds to the thickness of the prothallus [illegible] appearance. The apical cell may remain distinct and functional for a long period or it may be replaced by a row of few marginal cells. These divide in such a manner so as to cut off segments laterally as wall as towards dorsal

and ventral sides. This type of growth leads to the formation of an elongated heart-shaped prothallus with distinct cushion below the notch (Fig. 10·11, A). The cushion projects prominently on ventral side. The prothallus may continue to grow by means of this mar-

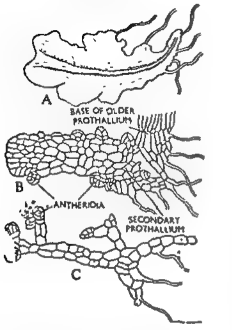

Fig. 10·11 (A—C). Prothalli of *O. claytoniana*. A. A young prothallus with a distinct apical notch. B. Old prothallus with secondary prothallus developed from an adventitious branch. C. A filamentous and a branching prothallus with antheridia. (After Campbell)

ventitious branches also grow by means of a two-sided apical cell. The rhizoids arise from swollen mid-rib portion on the ventral side and are unicellular in young prothalli, but become septate in older ones.

Sometimes the spores (*O. claytoniana*) develop into irregularly branched filamentous prothalli (9·12, C) that are either wholly male or are protandrous and produce archegonia very late. The male prothalli remain small and may be produced in larger numbers.

10·10, G). In this case no filament is pr... are not rare wh n the primary prothallus divides along three planes to form a mass of cells. An apical cell is soon established in this mass and by its activity gives rise to a flat and cordate prothallus. The central cushion is not very prominent in these species. The prothalli are dark green in colour.

Struct: ... mature prothallus of *Osmunda* is ... lorsiventral, green and a cordate or ... ·12, A). It varies in ... dicho- ... The ... cal ... *O.* ... lly ... ark ... di-

tions are monoecious, protandrous, flat and ribbon shaped and unbranched structures with a smooth or slightly wavy margin. Under

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O. regalis live long and reach a length of 4 centimetres. He also recorded dichotomy of the prothallus in this species.

SEX ORGANS

The monoecious prothalli are protandrous and bear antheridia after about two weeks (*O. cinnamomea*) to one month (*O. claytoniana*) of their development from the spore. The antheridia usually appear along the margins or on the ventral surface along

op either along
re scattered all
archegonia pro-
always produced

on the ventral side. Older prothalli possess both antheridia and
e of emergent type like most of the
many-celled wall. The archegonia,
t the neck is composed of 6 tiers of
cells instead of four (as usual number for the leptosporangiates). The antheridia in the exclusively male prothalli are either marginal or terminal.

Antheridia

Structure. The antheridia are of projecting or emergent type.
in position from
the prothallus.
The body of
of many-curved
triangular cell
at the apex of the antheridium or on one side, is the opercular cell

Development (Fig. 10·12, A—K). The antheridium develops from a single cell. The antheridial initial is cut off from a large superficial cell of the prothallus. In terminal antheridia the terminal cell of a branch becomes enlarged and divides by an oblique

10·12, B). The tetrahedral cell has its broad end facing outwards and the narrow end facing inwards. It cuts off segments along its three lower sides. These segments form the stalk of the antheridium.

The length and thickness of the stalk depends upon the number of segments cut off by the apical cell. Usually one or only a few

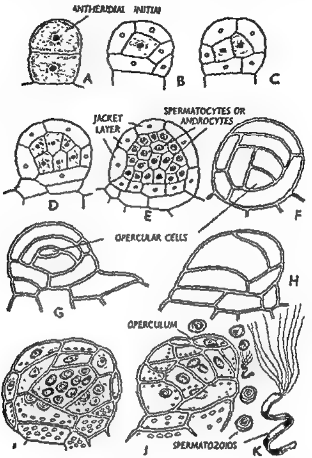

Fig. 10.12 *(A—J).* **Stages in the development of antheridium in** *Osmunda.* A—H. *O. cinnamomea;* I—K. *O. claytoniana* (After Campbell)

segments are cut off by the apical cell so that the stalk is either indistinct or very short. After the apical cell stops cutting segments from its three lower faces, it divides by a curved *periclinal* wall towards its outer broad face thus distinguishing an outer curved primary **jacket cell** and an inner **primary androgonial cell** (Fig. 10 12, B) The primary jacket cell undergoes *anticlinal* division to form two cells (Fig. 10 12, C). Both the jacket cells divide further by anticlinal and oblique walls to form the antheridial jacket. The antheridial jacket thus formed consists of a single layer of variously curved, chlorenchymatous cells (Fig. 10·12, D, E). A trangular cell or the **opercular cell** is formed by the division of the ... cells. The opercular cell is either apical or lateral

...s by now divided by repeated
... (100 or more) of androcytes or
... protoplasts of each androcyte
...ultiflagellate spermatozoid (Fig.
...ain within the androcyte walls

and escape by their gelatinisation after the dehiscence of the antheridium.

The position and mode of formation of the triangular opercular cell is quite similar to the eusporangiopsida. The emergent position of the antheridium and its origin from a single cell are leptosporangiate characters. The mode of wall formation and the formation of the stalk are characters quite peculiar to *Osmunda*. The number of androcytes is neither eusporangiate nor leptosporangiate. In the former they far outnumber *Osmunda* and in the latter they are few.

ARCHEGONIUM

Structure. The archegonia have projecting necks that project in a horizontal direction from the sides of the median cushion. The neck consists of 4 vertical rows of cells each row 6 cells in height, *i.e.*, it consists of 6 tiers of 4 cells each. The neck is, therefore, longer than the leptosporangiates. The neck encloses a single binucleate neck canal cell. The venter is embedded in the prothallus tissue and is not surrounded by its own wall. It contains a single ventral canal cell and a large egg cell. (Fig. 10·13, F).

Before fertilisation, the neck canal cell and the ventral canal cell disorganise and become mucilaginous. The mucilage absorbs water, swells up and forces the apical tier of cells apart, thus making an open
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:t

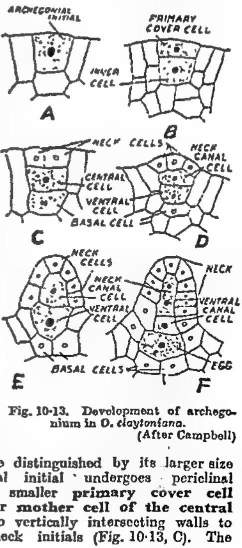


Fig. 10·13. Development of archegonium in *O. claytoniana*. (After Campbell)

Development (Fig. 10·13, A—F). The archegonium develops from a single superficial cell lying on the ventral side of the prothallus somewhere along the flanks of the central cushion. This cell is called the **archegonial initial** and can be distinguished by its larger size (Fig. 10·13, A). The archegonial initial undergoes periclinal division and cuts off an outer smaller **primary cover cell** (Fig. 10·13, B) and an inner larger **mother cell of the central cell.** The former divides by two vertically intersecting walls to form four diagonally arranged neck initials (Fig. 10·13, C). The

mother cell of the central cell divides transversely into an upper central cell and a lower basal cell (Fig. 10·13, C). The latter takes no further part in the development of the archegonium. It may divide once or twice to form cells that are indistinguishable from the surrounding prothallial cells. The neck initial divides transversely to form 6 or 8 tiers of neck cells (Fig. 10·13, D, E). The neck is straight or curved like [illegible] ntral cell divides into an upper [illegible] lower primary **ventral cell.** The former forms a single binucleate **neck canal cell** and the latter divides into an upper smaller ventral canal cell and a lower larger **egg cell.** The neck canal cell pushes in between the neck cells and its two nuclei may, in rare cases be separated by a wall to form two uninucleate neck canal cells.

EMBRYOGENY

As a result of fertilisation a diploid zygote nucleus or a synkaryon is established. It is surrounded by a dense cytoplasm,

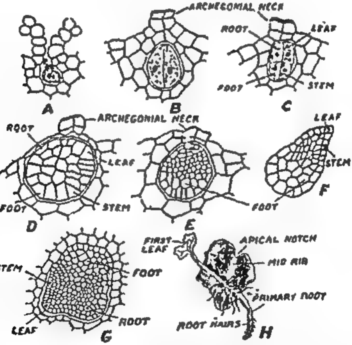


Fig. 10·14. Stages in the development of Embryo in *Osmunda*. A, C, D, F, H, *O. claytoniana*. B, E, G, *O. cinnamomea*. (A, C, D, F, H, After Campbell; B, E, G. After Cross)

which secretes a wall, thus establishing a diploid cell called the **zygote** or the **oospore.** It is lying in the venter and is protected by the surrounding prothallial tissue. The young oospore is the pioneer structure of the sporophytic individual. Its segmentation and further differentiation gives rise to the embryo which develops into the young sporophyte. These stages of development were studied by Campbell (1892) and Cross (1931).

The zygote divides by a wall parallel to the long axis of the archegonium (vertical wall) into two almost equal cells (Fig. 10·14), B). The two cells thus formed divide each by a wall at right angles to the first wall to form four cells (Fig. 10 15, C). This is the quadrant stage. The epibasal quadrants give rise to the leaf and the stem and the two hypobasal ones give rise to the foot and the root. The anterior epibasal quadrant forms the leaf and the posterior develops into stem. Similarly the anterior hypobasal quadrant gives rise to the root and the posterior to the foot. The quadrants divide transversely to form an octant stage. Subsequent divisions are not very regular. Cross (1931) stated that in *O. cinnamomea* the stem, leaf and the root develop from that half of the octant which is nearer to the archegonial neck. The foot develops from the other half. The foot is well developed and may perform haustorial functions. The root apical initial appears endogenously and by its activity gives rise to the primary root. The development of the embryo is slow and it retains its globular form for a sufficiently long time.

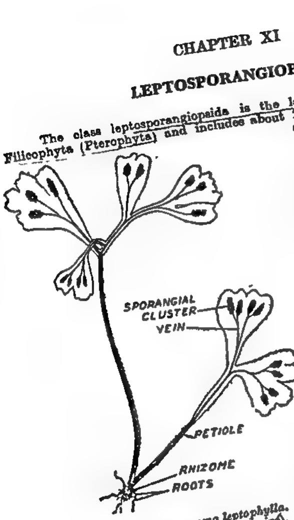
The leaf initial makes its appearance as three-sided apical cell in the anterior epibasal octant. The young leaf soon appears as a conical protuberance (Fig. 10·14, F) on one side. The first leaf does not come out of the surrounding prothallial tissue until quite late. The tetrahedral root apical cell grows into a massive primary root. The stem apex appears on one side of the leaf apex in the posterior epibasal half and grows into the underground stem after the primary leaf and primary root had established themselves. The primary leaf has broad lamina with irregular margin. The venation is furcate. It possesses stomata on both the sides. The vascular bundle of the petiole is of collateral type and that of the root is diarch. The vasculature of the young rhizome is protostelic and becomes dictyoxylic at a later stage (after producing 3 or 4 leaves).

Brown (1920) and Sarbadhikari (1939) reported apogamy and apospory in *O. regalis* and *O. javanica*. The sporophytes arise from the gametophytes without the formation of sex organs aud subsequent fertilisation. Such sporophytes have the same genetic constitution *as the gametophyte. Their formation has been observed under* natural as well as experimental conditions. Sarbadhikari (1939) also reported aposporous production of gametophytes from the sporophytic tissue (see Chapter I). He found that in *O. javanica* the aposporous gametophytes produced antheridia but no archegonia. The sporophytes developed as vegetative outgrowths from the tissue of the prothallus.

CHAPTER XI

LEPTOSPORANGIOPSIDA

The class leptosporangiopsida is the largest class of the division Filicophyta (Pterophyta) and includes about 232 genera and about 8,680 species. They grow luxuriantly in the tropical rain forests but are also met with in the temperate regions of the world. They love to grow under moist, cool and shaded places but forms growing under extremes of habitat condition are not rare. A number of them grow under xerophytic conditions (*Drymaria*, *Hypodematium crenatum*, *Dryopteris chrysocoma*. *Adiantum incisum*, *Woodsia elongata*, *Cheilanthese chrysophylla*, *Lepisorus nudus*); a few are hydrophytes (*Marsilea*, *Azolla*, *Salvinia*) and the majority are mesophytic. They also form a dominant epiphytic vegetation in the forests. Majority of them are perennials and only a few are annuals. They range in size from extremely small forms like *Anogramma leptophylla* which is almost 4·5 cm. in height (Fig. 11·1) to huge tree like forms of the Cyatheaceae. Their abilty to live under varied environmental conditions and the property of the leaf to perform a dual function of photosynthesis and reproduction are considered to be responsible for their widespread occurrence. A detailed account of the general features of these ferns is given in Chapter 8 and it is needless to dwell them again in this chapter.



(Fig. 11·1. *Anogramma leptophylla*. A complete plant (1½ natural size).

The class Leptosporangiopsida has been divided by Reimers (1954) and Smith (1955) into three orders. These are, (i) Filicales (ii) Marsileales and (iii) Salviniales. These have been recognized as separate orders on account of the nature of spores (whether homosporous or heterosporous) types of sporocarps, reduced and indistinct gametophytes and their habits. The last two orders are heterosporous and aquatic. Christensen (1938) divided this class into two orders (Filicales and Salviniales). He included the Marsileales

in a separate family Marsileaceae and included it under the order Filicales. Marsileales deserve the rank of a separte order as they possess a number of distinct features which take them away from the homosporous forms. In this text the classification proposed by Reimers and Smith is followed.

Order Filicales

most all the ed by about by Reimers Matoniaceae, (iv) Hymenophyllaceae, (v) Dicksoniaceae, (vi) Cyatheaceae and (vii) Polypodiaceae. Nayar (1962) reported a wide range of stelar arrangement in *Adiantum*. He regarded this genus as an isolated form and suggested its inclusion in a separate family called Adiantaceae. Nayar and Kazmi (1962) also proposed that the genus *Plagiogyria* is an isolated and a primitive genus which should be placed under a separate order Plagiogyriales.

Holttum (1949) divided the order into 10 families. These are

19 families.

Family : POLYPODIACEAE

There is no general agreement regarding the limits of the family. A number of systems of classification have appeared but the taxonomy of this family remains undecided. It is not within the scope of this volume to discuss all these systems. The system proposed by Christensen (1938) has been followed in this text. He sub-divided the family into fifteen sub-families and included about 170 genera and 7,000 species. He, however, agreed that these sub-families can be raised to the status of families. All these sub-families are grouped together because their representatives possess sporangia with long stalks, biconvex capsules and vertical and incomplete annulus

The family is characterised by the following features :

1. They are varied in the habitat and may be mesophytic, xerophytic, epiphytic and aquatic.

2. The leaves may be simple, pinnately compound or even palmate and vary in size from a few centimetres (*Annogramma leptophylla*) to a metre or more in length.

3. The rhizomes may be siphonostelic (*Adiantum sp.*), solenostelic (*Pteris sp*, *Adiantum sp.*), dictyostelic (*Dryopteris*) or polycyclic (*Polypodium*, *Pteris*).

4. The roots may be diarch, triarch, or tetrarch. Polyarch roots are also found.

5. The sporangia are grouped in sori that may be naked *(Polypodium)*, or protected by indusium *(Dryopteris)*. The indusium may be false *(Pteris, Adiantum)* or true *(Dryopteris)*.

6. The sori are usually mixed. The sporangia have vertical and incomplete annulus. There is a distinct stomium.

7. The number of spores per sporangium varies from 32 to 64. The spores are bilateral or tetrahedral in shape and may be with or without a perispore.

8. [illegible]

9. The sex organs show no diversities in their structure and development. The antheridia have a single cap cell except in *Woodsia*, which has two cap cells. In *Annogramma leptophylla* the archegonia develop on specialised and tuberous branches called the archegoniophores.

10. [illegible] ...ere is no suspensor [illegible] long axis of the archegonium.

Detailed life histories of *Dryopteris* (sub-family *Dryopteridioideae*), *Pteridium*, *Pteris* (sub-family *Pteridioideae*), *Adiantum* (*Gymnogrammeoideae*) and *Polypodium* (sub-family *Polypodiodeae*) are discus. in this text.

Sub-Family DRYOPTERIDOIDEAE Christensen

The sub-family is characterised by the following features :—

1. The sori are superficial and may be borne on the vein or on vein endings and may be with or without indusium. The sori arise on raised receptacles on the ventral side of the pinna or pinnule.

2. The sporangia are mixed and have a distinct long stalk that is made up of three rows of cells. In *Dryopteris* the stalk bears a water gland.

3. The number of spores per sporangium varies from 32 to 64. The spores are usually bilateral and have perispore.

4. The gametophytes are monoecious and epiterranean. They are green, cordate, dorsiventral and bear sex organs on the ventral side.

5. The [illegible] type with short and bent necks [illegible] wall made up of three cells. [illegible]

6. The stelar organisation is dictyostelic.

7. The rhizome is densely covered with hair like or broad scales called the ramenta. In *Goniopteris* the scales are branched and *stellate*.

8. The leaves may be simple or compound and are circinately coiled in a bud condition. The venation may be reticulate or dichotomous.

The sub-family includes 25 genera (Christensen, 1938) and 1,500 species. *Life history of Dryopteris* Adanson is discussed in this text.

DRYOPTERIS Adanson

The genus *Dryopteris* includes about 250 species that are distributed in the North temperate regions, East Asia and Africa,

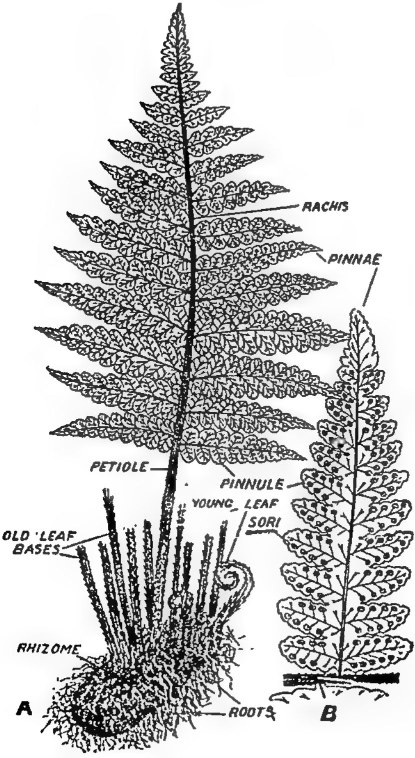


Fig. 11-2. *Dryopteris [illegible].*
A. Sporophyte showing habit.
B. A pinna as seen from ventral side. Note the kidney-shaped sori.

tropical and sub-tropical reginos of the world. About 25 species have been recorded in India All of them grow in the Western and North Western Himalayas and around Simla. *Dryopteris ramosa* and *D. blanfordii* are very common in Kashmir. *Dryopteris chrysocoma* is extremely common (Fig. 11·2) in India and grows on exposed places and hill tops between 1,540—2,700 metres above sea level. It can also grow well under moist and shaded environments. It is exceptionally common along the margins of forests in the North Western and Eastern Himalayas.

SPOROPHYTE

(a) Morphology

The sporophyte ... rhizome that is fixed to ... roots. The only above ... that vary in length from 15 centimetres to 50 or more. The rhizome is generally creeping (*D. rigida*, *D. fibrillosa*) and dorsiventral. In *D. chrysocoma* and *D. filix-mas* it is short, stumpy and obliquely placed or semi-erect ... h brown, soft, broad ... sparingly branched. ... h bases of old and ... uneven. The apex ... closely packed young leaves that form ... leaves a little behind the apex are ...). The older leaves unfurl into a ... the frond. The leaves are crowded

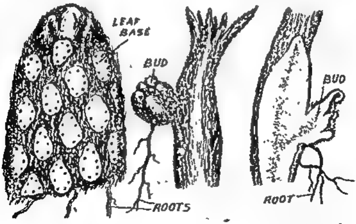


Fig 11 3. *Dryopteris.* Rhizome with leaf bases removed ... petiole bearing ... oot. ... section of the petiole bearing the bud. (After Sachs)

around the apex and form a crown giving a 'basket like' form to the plant. Their arrangement is acropetalous, *i.e.*, the younger are

near the apex and the older behind. The crown like appearance is due to their nearness to each other. The young leaves are profusely covered with chaffy scales or ramenta. As the leaves grow older the the scales fall away and are found only on the petiole. The roots arise from the lower or the ventral side of the rhizome and are thin, black and wiry structures.

The leaves are pinnate compound and may be unipinnate or bipinnate (*D. rigida*). In *D. erubescens* and *D. chrysocoma*, the pinnae are deeply cut or incised into pinnules. Such leaves are [illegible] pinnae near the base [illegible]ger up to the middle [illegible] up to the apex of the leaf. This gives the leaf a spindle-shaped appearance. The margins of the pinnules are also incised and may appear dentate or crentate. The whole leaf may vary in size from 12 cm. to 55 cm. in *D. chrysocoma*. The venation is furcate and open. Each pinnule is traversed by a distinct midrib which bears furcate lateral veins. In *Dryopteris cochleata* there is segregation of fertile and sterile pinnae. In other species there is no such differentiation.

(b) Anatomy

Rhizome. The rhizome is profusely clothed with ramenta and bases of older leaves. The latter give it an irregular appearance (Fig. 11·4). There is a distinct epidermis which in older rhizome becomes sclerenchymatous. The epidermis may be perforated with stomata. It is covered with a distinct cuticle. Next to the epidermis is a few layered hypodermis. It is made up of sclerenchymatous cells that form a peripheral strengthening cylinder (Fig. 11·[illegible]d tissue in which lie [illegible] leaf and root traces. [illegible]e ring of the meri[illegible] of the ground tissue internal to the meristeles and forming the core of the rhizome is called the pith. The cells composing the entire ground tissue are parenchymatous with cellulose cell walls and store food material in the form of starch grains.

The parenchymatous ground tissue in which the whole vascular system of the plant is embedded serves various functions. It performs storage functions in the stem and absorbing and translocating system in the roots. In the leaves it serves to manufacture food and then pass it on to the conducting system. Besides these, functions of gaseous exchange, transpiration and numerous other physiological phenomena take place in these tissues surrounding the vascular system.

The vasculature of *Dryopteris* is a typical *dictyostele* with *meristeles* of varying sizes arranged in an interrupted and irregular ring (Fig. 11·4, A). The number of meristeles is also variable. Their shape may be circular, elliptical or oval, sometimes curved and reniform The whole stele if dissected out of the groun[d] tissue appears to be a cylindrical meshwork of vascular strands (Fig. 8·6).

It gives off leaf traces to the leaves and from the bases of the petioles the leaf trace bundles give off vascular strands to the roots.

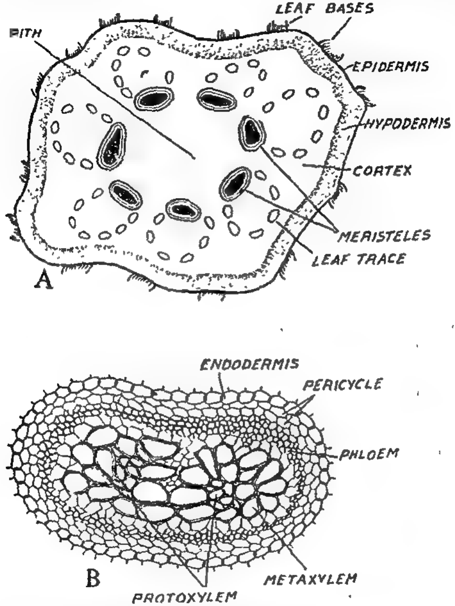


Fig 11·4 (A—B). *Dryopteris chrysocoma*
A. Diagrammatic t.s. of rhizome illustrating internal structure;
B. A meristele detail.

The stelar system of *Dryopteris* is, therefore, an inter-connecting conducting system that extends throughout the plant.

A dictyostele is derived from the amphiphloic siphonostele by the appearance of overlapping leaf gaps in the former. The leaf traces departing to the fronds leave these parenchymatous gaps in the continuous vascular cylinder and make it perforated.

A single meristele (Fig. 11·4, B) is bordered by a single layer of endodermis, whose cells have distinct casparian strips. Next to it is a single layered pericycle that surrounds the phloem tissue. Phloem has protophloem which forms a single layer of small sieve elements and parenchyma, next to the pericycle, and metaphloem which forms a layer or two of larger sieve cells and phloem parenchyma. The protophloem has been seen to develop (Ching, 1927) from a mother cell layer that also gives rise to pericycle and endodermis. In a longitudinal section (Fig 11·5) the sieve tubes of the metaphloem appear to be spindle-shaped in outline and bear **sieve plates** on their lateral walls. Companion cells are lacking. Phloem parenchyma is present and consists of elongated and thin walled cells that store food. Vessels are absent. Xylem is mesarch and forms the solid centre of the meristele (Figs. 11·4; B, 11.5).

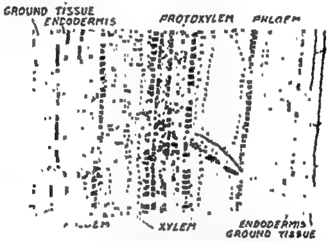


Fig. 11·5. L.S. rhizome of *Dryopteris chrysocoma* showing the structure of a single meristele.

The small protoxylem tracheids are surrounded by large metaxylem tracheids with few cells of xylem pa[illegible]a separating the two. [illegible] e whereas those of [illegible] elongated and are [illegible] other (Fig. 11·5) giving a ladder like or scalariform appearance. Such pits are designated as **scalariform pits** and are characteristic of the ferns. Sometimes the closing membranes of the pits lying across the cross walls of the tracheids become absorbed and establish an open connection between the two tracheids lying one above the other. Such a condition simulates true vessels and is of rare occurrence in *Dryopteris* but common in *Pteridium aquilinum*. The tracheids are spindle-shaped. The xylem and phloem are separated by a layer or more of **xylem parenchyma or conjunctive parenchyma.**

There is no secondary growth in the rhizomes of ferns and the concentric meristeles are of limited growth.

Root. The structure of the root presents no variations among the polypodiaceae. A transverse section (Fig. 11·6) reveals an outer-

most piliferous layer. The cells of this layer are thin-walled and may bear unicellular hair. Next to this is the wide cortex which is clearly distinguishable into an outer parenchymatous cortex and an inner sclerenchymatous cortex. The latter is the chief strengthening

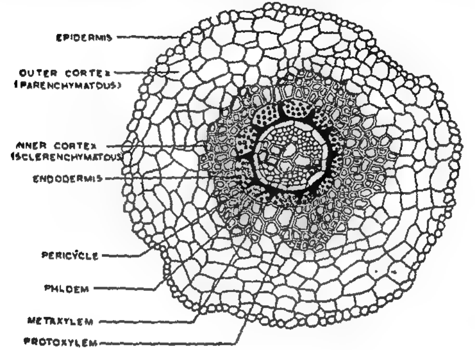


Fig. 11·6. T.S. root of *Dryopteris chrysocoma*.

tissue of the root and completely surrounds the central stele. Next to the inner cortex is a complete and distinct layer of endodermis. It is made up of a single layer of thin-walled cells with casparian bands on the radial walls. One or two layers of thin-walled cells next to the endodermis constitute the pericycle. The stele is diarch and consists of a central plate of xylem with smaller tracheids of proto- [illegible] Phloem forms [illegible] There is no pith [illegible], resembles the seed plants in its primary organisation, there being no secondary growth in the ferns.

The lateral roots originate opposite the protoxylem groups from definite cells of the endodermis and are thus endogenous.

Leaf. The structure of leaf lamina and the petiole offer greater variations among the polypodiaceae.

(i) **Lamina** (Fig. 11·7). A cross section through the sterile [illegible] and lower epidermal layers with [illegible] the *epidermis contain chloro-* [illegible] ed to the lower surface (in plants [illegible] be present on both the

surfaces (in shade plants). The mesophyll is not distinguished into palisade and spongy parenchyma. The cells of the mesophyll are thin-walled, chlorenchymatous and loosely arranged, enclosing small and large intercellular spaces among them. The cells of the meso-

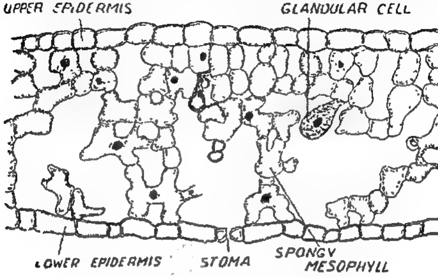


Fig. 11·7. V.S. through lamina of the sterile pinnule of *Dryopteris*. (After Bower)

phyll immediately below the upper epidermis are either slightly lobed or not at all lobed and enclose smaller intercellular spaces whereas in the centre they are comparatively larger and irregularly lobed and enclose larger intercellular spaces. Some of the mesophyll cells bear distinct glandular cells. These are water glands (Fig. 11·7) and store water to be utilised under conditions of stress or dessication.

The vascular bundle of the midrib of the pinnule is either concentric or bicolateral (phloem on both the sides of the xylem strand) whereas in the smaller veins it is collateral with phloem present only towards the lower side of the xylem. The collateral condition results due to the disintegration of the phloem elements above the xylem strand. A distinct endodermis or the bundle sheath encircles each vascular strand. The cells surrounding the vascular bundles are compactly arranged and extend as such to the upper and lower epidermis. These are often called bundlesheath extensions.

(iii) Petiole. A trasnverse section of the petiole near its base reveals the following structure (Fig. 11·8).

The outer epidermal layer completely surrounds a sclerenchymatous hypodermis which consists of 2 to 7 layers of lignified cells. The rest of the tissue is parenchymatous ground tissue in which lie embedded a number of meristeles that are arranged in horse-shoe-like manner (Fig. 11·8). The meristeles are almost round in shape and are of varying sizes.

Each meristele (Fig. 11·9) has a structure similar to that of the stem meristele. The xylem is mesarch 'and is surrounded by

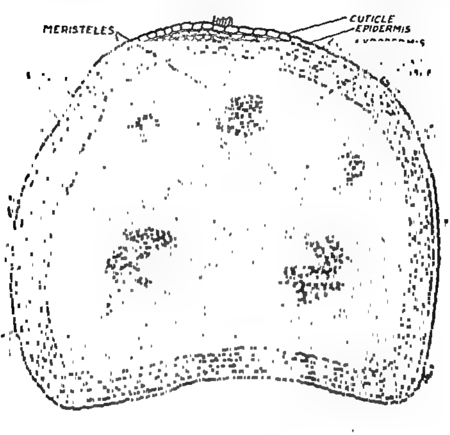


Fig. 11 8. T.S. through basal region of petiole of *Dryopteris chrysocoma* showing detailed internal structure.

phloem. The two tissues are separated by a layer of conjunctvie parenchyma or xylem parenchyma. There is a distinct pericycle and endodermis.

APICAL GROWTH

(a) **Rhizome.** The rhizome grows by means of a single apical cell in the young sporophyte. Later a group of cells [redacted] visible at the stem tip. These cells form a single layer and have a single two-sided large cell flanked on either side by its derivatives. The large cell is the apical cell and its derivatives are called the prismatic cells (Wardlaw, 1943). These together constitute the apical meristem. These cells divide and redivide to form a group of actively dividing cells which later give rise to a cap-like zone of prestelar cells or the incipient vascular elements. These give rise to stelar tissue of the rhizome. Immediately beneath the stelar cap [redacted] the cone of parenchyma cells that constitute the pith (Fig. 11·10).

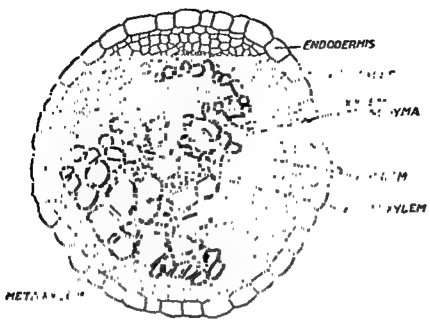


Fig. 11·9. *Dryopteris chrysocoma*. A single meristole from the petiole as seen under higher magnification.

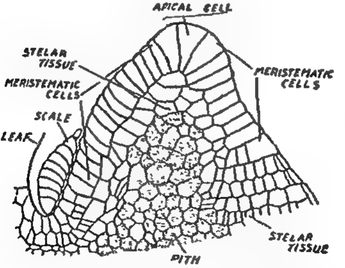


Fig. 11·10. L.S. Rhizome of *Matteuccia struthiopteris* showing apical organisation.
(After Wardlaw)

(*b*) **Leaf.** It has a single two-sided apical cell that cuts off, in a regular sequence, two rows of segments.

(*c*) **Root.** The root grows by means of a single tetrahedral apical cell that cuts segments on all its four sides. The primary tissues of the root are derived from the segments cut off along the three lateral sides. The fourth upper side cuts off segments that give rise to the root cap.

VEGETATIVE PROPAGATION

A detailed account of the methods of vegetative propagation has been given in Chapter 8. In *Dryopteris* the sporophyte reproduces vegetatively by the death and decay of older portions of the rhizome and separation of younger branches which root themselves as independent plants and produce young leaves. *Dryopteris* has also buds developed a little distance up the petiole (Fig. 11·3). These buds are capable of producing roots and establishing themselves as independent young plants Such buds have also been induced experimentally on the young and old leaf primordia of *D. dilatata* (Wardlaw, 1943, 1947, 1949; Cutter, 1954, 1956, 1957, 1963).

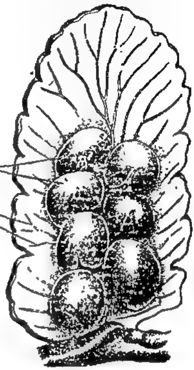


Fig. 11·11. A pinnule of *Dryopteris chrysocoma* as seen from ventral side. Note the sori and their position.

REPRODUCTION

(*a*) **Sporophylls and Sori.** Th[illegible] to [illegible] ll [illegible] r-forming the twin function of [illegible] Th- [illegible] y part or on the whole of the leaf.

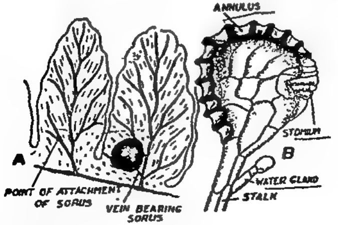


Fig. 11·12. *Dryopteris chrysocoma*.
A. Fertile pinnules showing the position of sorus on a vein.
B. A sporangium.

D. coc ,
shows
part of
of gree
called the **sori** (sing. sorus).

A sorus is a group of sporangia and in *Dryopteris* it is protected by sorus is borne singly unc vein (Figs. 11·11 and 11· cle and continues its course forward beyond the sorus. A mature sorus is, therefore, borne on the vein and not at its end. The vein provides the sorus with its necessay nourishment. The sorus arises on a distinct semi-lunar receptacle.

The young receptacle arises as a group of cells a little inwards from leaf margin (Fig. 11·13, A). Such a condition can be seen

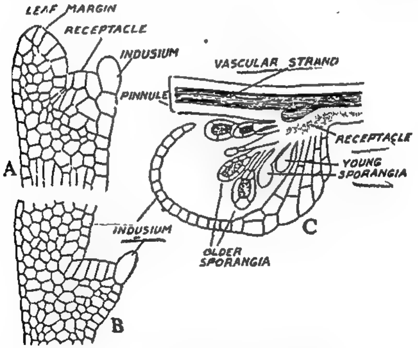


Fig. 11·13. Receptacle and sorus of *Dryopteris*.
A. V.S. Young sorus *D. filix-mas* cut in the direction of vein. The receptacle and the indusium are shown.
B. An older stage of A.
C. V.S. Young sorus showing well developed indusium and sporangia in various stages of development.
(After Bower)

in a longitudinal section cut in the direction of the vein (Fig. 11·13, A, B, C). These sections clearly show that the receptacle is lop-sided from the time of its inception and the indusium starts developing very early. The sporangia start developing when the receptacle is completely overarched by the indusium (Fig. 11·13, C). The young

receptacle shows basipetalous development of the sporangia (Fig. 11·13, *C*), but this sequence soon changes to the mixed type as the sorus grows in age. The mature indusium is *kidney-shaped*.

A vertical section of the fertile pinnule *cuts the vein bearing* the sorus, in a transverse plane and shows the following structure (Fig. 11·14).

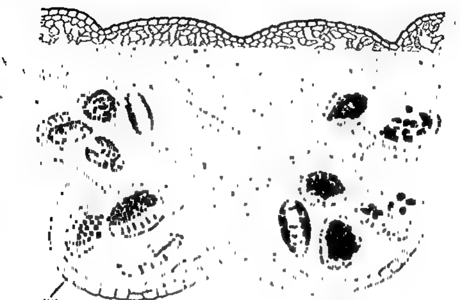


Fig. 11·14. V. S. sorus of *Dryopteris chrysocoma.*

[illegible] shows the usual upper and lower [illegible] ophyll of loosely arranged cells [illegible] receptacle is seated upon the [illegible] placenta-like [illegible] the receptacle and supply it with the required nutrition. The indusium arises from the receptacle and overarches the sporangia that are attached to it by means of *long stalks, which invariably bear* the water glands (Figs. 11·12, 11·14). The indusium, in such a section, appears to arise from a central stalk like portion and overarches the receptacle equally on either side.

(*b*) Sporangium

(*i*) Structure. The sporangium in the polypodiaceae presents a remarkably uniform structure. It consists of two parts; the **stalk** or the **pedicel** and the **capsule** or the **spore case** (Fig. 11·12, B). The stalk is composed of three rows of elongated cells. It bears a water gland (Fig. 11·12, B). The capsule or the head of the sporangium is more or less oval in shape and appears like a biconvex lens. It has a single-layered wall enclosing *forty-eight bilateral* spores. The cells of the wall along the margin of the sporangial

head become thickened along their inner and radial walls to form an almost vertical row of indurated cells. This is the annulus.

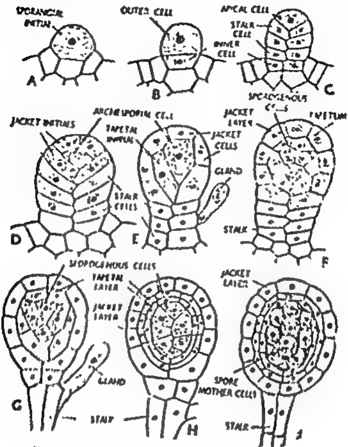


Fig. 11·16. (A—I). *Dryopteris chrysocoma*. Stages in the development of sporangium.

the development. The upper or the sporangial cell divides by three oblique peripheral walls (Fig. 11·15, C), which enclose tetrahedral apical cell. The cell cuts off segments along its three sides (only two are shown in the figure). These segments give rise to the three vertical rows of sporangial stalk (Fig. 11·15, D—E). One of the distal stalk cells gives out a lateral protuberance (Fig. 11·15, E) which develops into a water gland. It is characteristic of **Dryopteris** sporangium. The last three segments act as the three **primary jacket initials** (Fig. 11·15, D). The apical cell now stops cutting off segments laterally. It divides along its fourth or upper side by a periclinal wall. This is the fourth **primary jacket cell.** The four jacket initials enclose a triangular **archesporial cell,** which divides periclinally (Fig. 11·15, E) to form 4 **primary tapetal cells** (only three visible in the figure). They divide periclinally so as to form two layers of primary tapetal cells (Fig. 11·15, G). The **central cell** enclosed by the tapetal cells is called **primary sporogenous cells** (Fig. 11·15, G). The jacket initials and the tapetal cells divide anticlinally to form : (*i*) a single-layered wall of the sporangium and (*ii*) two layered tapetum (Fig. 11·15, H). Meanwhile sporogenous cell has divided to form twelve **spore mother cells** (Fig. 11·15, I). These cells undergo meiosis to form tetrads (Fig. 11·16, A, B) of haploid spores, which number forty-eight. The tapetal cells disorganise and form a nutritive fluid. The unused fluid may stick around the spores and form an outermost layer called the **perispore.**

Prior to sporogenesis the spore mother cells round off and separate from each other (Fig. 11·15, I). The tapetal cells start disorganising. The diploid nuclei of the spore mother cells undergo meiosis to form 4 haploid nuclei in each mother cell. As a result of simultaneous laying down of the walls between the nuclei, tetrads of haploid cells are formed (Fig 11·16, A, B). The haploid cells are called the spores and the process of their formation is called **sporogenesis.** These haploid spores are also called **meiospores.** The spore mother cells are, therefore, the last structure of the sporophyte generation. The meiospores are the pioneer structures of the gametophyte generation.

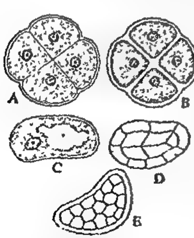


Fig. 11·16. (A—E). Spore tetrads and spores of *Dryopteris chrysocoma*.
A—B. Tetrads of spores.
C. Spore in section.
D—E. Spores as seen in surface view.

(*iii*) **Dehiscence of the Sporangium** (Fig. 11·17). The sporangia usually open in dry weather and the enclosed dust like spores are ejected out forcibly. The spores are produced in millions by one plant and are dark coloured, dusty

and minute. T ... :ned in the dehiscen ... ter. As a result the ... more than the thick ... into the cavities of the annulus cells. This generates a combined suction force all along the vertical annulus. As a consequence of this ... cells rupture and are torn apart. ... the sporangial wall straightens ... is back (Fig. 11·17, B). This movement of the annulus exposes the spore mass and scatters them with some force. Some spores remain clung to the annulus. Finally a stage is reached when the cohesive force of the water within the annulus cells decreases and the sucked in walls are pushed outwards with an explosive force. This leads the annulus and a portion of the wall to snap back to its original position (Fig. 11·17, C). During this process the spores clinging to the annulus are also thrown off into the air. Dehiscence of the sporangium is effected only during the dry weather. as loss of water is essential for setting up the required force.

GAMETOPHYTE GENERATION

Spores. The spores are trilete, bilateral, minute, dusty and dark coloured structures. The spore has an outer spore coat called the exine and an inner thin and delicate intine. The exine is covered by a *perine* (perispore). The exine is further made up of two layers. The is outer called the **ectine** and the inner known as the **endine.** The ectine is made up of radially elongated rods called the **columellae.** The upper free ends of columellae are fused to form a layer called the **tegillum.** The tegillum is reticulate in *D. chrysocoma* (Fig. 11·16, D. E). The two spore coats enclose a scanty amount of cytoplasm and a single nucleus (Fig. 11·16). The cytoplasm stores food but has no chloroplasts.

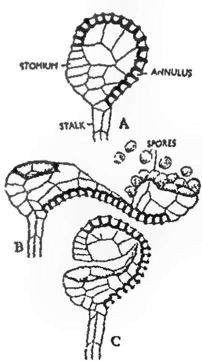


Fig. 11·17 (A—C). Stages in the dehiscence of the sporang...

Germination of the Spore (Fig 11·18). Moisture and suitable temperature are essential for spore germination. The spore absorbs moisture and increases in size. The nucleus becomes prominent. The exine ruptures along the trilete aperture (triradiate mark) and the intine protrudes out along with the enclosed contents (Fig. 11·18, B) in the form of a small germ tube. The germ tube elongates, its cytoplasm

chloroplasts and it divides into a small lower and a large upper cell. The lower cell loses chloroplasts and acts as the **primary rhizoidal cell** (*Fig.* 11·18, C). It gives out the first rhizoid which establishes contact with the substratum. *The upper cell or the* ***prothallial cell*** contains many chloroplasts and by further elongation and transverse division develops into a green, uniseriate filament 3—5 or even more cells in length (Fig. 11·18, D). Under favourable conditions the filament develops into a flat, cordate and a dorsiventral prothallus. The terminal cell of the filament divides by two oblique and intersecting walls to cut off a two-sided apical cell (*Fig.* 11·18, *E*). *The lower* cells of the filament may or may not divide further. The segments cut off by the apical cell divide and *redivide to form a green* and flat plate of cells, one cell in thickness (Fig. 11·18, F). The young segment cut off by the apical cell divide rapidly and cells cut off towards *their outer* face *overgrow* the apical cell, which is now lying in a concavity or a *depression*. The *depression* becomes deeper during further growth and gives a heart-shaped appearance to the prothallus (*Fig.* 11·18, F). The single apical cell is replaced by a series of two or more *marginal* meristematic cells so that further growth *takes* place by *the division of* a *group* of marginal meristematic cells and not a single apical cell. The apical notch (*Fig.* 11·18, F). has become sufficiently deep by now. The cells cut *off* by the marginal *meristem* lead *to* the formation *of a central* cushion *of* cells posterior to the apical notch. The cushion is two or more cells thick, whereas the wings of the prothallus remain one cell in thickness. *The* prothallus has, by now, *assumed* a dorsiventral *symmetry*. It has a distinct anterior side

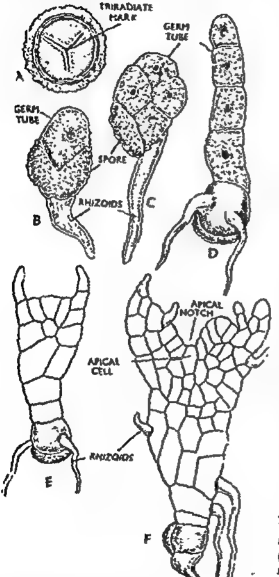


Fig. 11·18 (A—F). *Dryopteris filix-mas.* Stages in the germination of spore and formation of young prothallus. (*After Kny*)

(towards the apical notch) and a narrow posterior end. Numerous unicellular rhizoids arise from the ventral side of the posterior end. They grow into the soil and besides anchoring the prothallus, also absorb water and other nutrients from the soil.

Under unfavourable circumstances and crowded conditions the spore germinates to give rise to a branched and a filamentous prothallus (Fig. 11·19, A). Such prothalli are starved and bear only male sex organs (antheridia). If transferred to favourable [illegible] condition is lost and a [illegible] can again produce both [illegible]

[illegible] mature prothallus or [illegible] existence under moist [illegible]d dorsiventral thallus. [illegible] by means of numerous unicellular rhizoids. The rhizoids arise from the ventral side

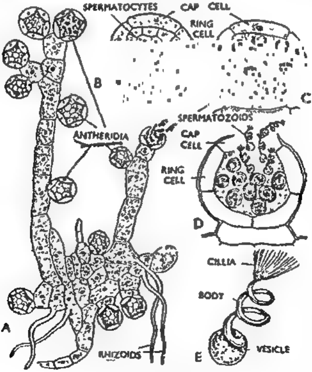


Fig. 11·19 (A—E). *Dryopteris filix-mas.*
A. A filamentous prothallus bearing antheridia only.
B—D. Antheridia showing structure and dehiscence.
E. A spermatozoid (After Kny).

and are mostly restriced to the posterior narrow end. It is normally unbranched and heart-shaped in outline with a deep notch at its anterior end. Below the notch lies the apex which consists of a number of meristematic cells. Behind the apex the central portion of the prothallus is more than one layer

of the cells in thickness and forms a distinct cushion. The thickness of prothallus lateral to the central cushion is only one cell layer. The mature cells of the prothallus are green in colour, thin-walled, with a peripheral layer of protoplasm surrounding a big central vacuole. The nucleus and the chloroplasts are embedded in the lining layer of cytoplasm. The cells are compactly arranged and have no intercellular spaces between them. The prothallus may reproduce vegetatively by gemmae.

Sex organs. The prothallus is monoecious and bears multicellular and jacketed sex organs that arise on the ventral side.

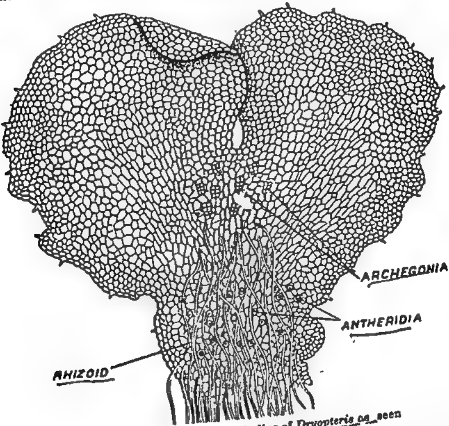


Fig. 11·20. A mature prothallus of *Dryopteris* as seen from ventral side. (After Kny)

The male sex organ is called the **antheridium** and the female is known as an **archegonium**. In rare cases the prothalli are dioecious, but such prothalli may bear archegonia at a later stage. The ventral position of the sex organs exposes them directly to moist air and water which are necessary for their development and dehiscence. The antheridia are emergent and develop among the rhizoids. The archegonia have their necks produced and bent towards the antheridia (Fig. 11-20). They are borne on the central cushion, behind the apical notch. The monoecious prothalli are always **protandrous**, *i.e.*, antheridia appear earlier than the archegonia. This device is helpful in bringing about cross fertilization.

Antheridia

(*a*) **Structure.** The antheridia are small, sessile and globular structures that project above the lower surface of the prothallus, among the rhizoids. Each antheridium consists of a wall made up of three tabular cells (Fig. 11·19, B, C) and a group of about 32 spermatozoids that are enclosed within the wall. The three cells of the wall are : an **opercular cell** or the **cap cell, second ring cell** and the **first ring cell.** The cap cell is also called the cover cell and forms a lid which on being lifted allows the spermatozoids to escape. The second ring cell or the circular cell forms the middle portion of the wall and extends completely around the antheridium. The third cell is the funnel-shaped first ring cell. It extends around the basal portion of the antheridium. Besides these three cells, there is a fourth cell at the base of the antheridium. This is the **basal cell** and may be regarded as a single-celled stalk. The wall cells in a mature antheridium contain little cytoplasm, few chloroplasts mitochondria and vacuoles full of phenol compounds.

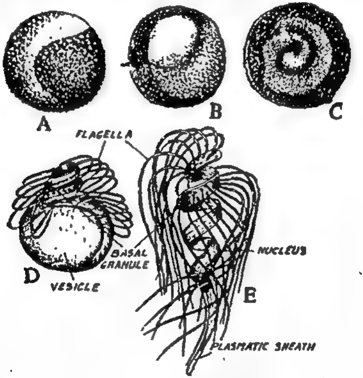


Fig. 11·21 (A—F). Spermatids and spermatozoids of *Dryopteris*. A. Coiled [illegible] end of [illegible] sper- [illegible] eris. [illegible] been [illegible] after

(*b*) **Structure of spermatozoid.** The protoplast of each spermatogenous or sperm mother cell produces a single large, coiled spermatozoid or antherozoid which is largely nuclear in origin and

has a prominent posterior vesicle (Fig. 11·19, E) The spermatozoids escape from the antheridium while enclosed (Fig. 11·21, C) within a membrane (Dracinschi). They become free immediately after their liberation. The liberated spermatozoid has 2½—3 spirals which rest on a vesicle (11·21, D and E). The vesicle has a homogeneous ground substance with fat globules, 4—6 plastids and a number of smaller granules embedded in it. The coiled portion is nuclear in origin. It moves along an irregularly spiral path and discards its vesicle. After discarding the vesicle, the spermatozoid elongates and becomes coiled into 4—5 spirals (Fig. 11·21, E). It is now ready to enter the archegonium. *At this stage the spermatozoid is without a vesicle and* consists of a motor apparatus and a nucleus. The nucleus extends [illegible] (Fig. 11·21, E) beginning [illegible] until it occupies the entire [illegible] point. It is surrounded by a protoplasmic sheath [illegible] of a thread at posterior end. The flagella arise from the basal granules.

(c) **Dehiscence.** The antheridium dehisces in the presence of water, which it absorbs. Consequently the mucilaginous walls of the spermatids swell and antheridial wall cells become turgid. The tension thus set up is relieved by the cap cell either being tilted upwards or detached (11·19, *D*). The spermatozoids enclosed within a thin membrane extrude out en-masse. The extrusion of the spermatozoids is further assisted by the inward swelling and shortening of the wall cells.

(*d*) **Development** (Fig. 11·22, A—E). The antheridium develops from a single superficial cell *(mother cell) that bulges out* and *forms a papilla like outgrowth.* It is cut off from the mother cell by a transverse wall (Fig. 11·22, B, a—a) This projecting cell is the antheridial initial. The antheridial cell divides by a curved periclinal wall (Fig. 11·22, C) into an outer **dome cell** or **central cell** and a lower **first ring cell.** This wall varies in curvature. In *Dryopteris* it curves so much that it almost touches the basal cell and looks like a funnel. The dome cell or the central cell divides by another curved wall (Fig. 11·22, D, 2—2) into an outer or peripheral **jacket cell** and a central **primary androgonial cell.** The jacket cell divides again by a curved periclinal wall whose bulge touches the second wall (2—2) and distinguishes an apical **cap cell** or **cover cell** (Fig. 11·22, E, 3—3) from a **second ring cell.** Thus constituted, the wall of the antheridium has three cells. It encloses a primary androgonial cell that

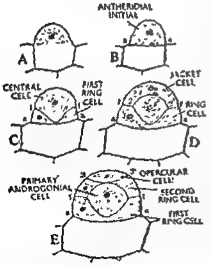


Fig. 11·22. Stages in the development of an antheridium (based on Davie)

divides and redivides into 16 sperm mother cells which divides further into 32 spermatids, whose protoplasts metamorphose into multiflagellate spermatozoids. The sperm mother cells lose their chlorophyll and have dense cytoplasmic contents and distinct nuclei. Later two polar granules appear on either side of the nucleus. The sperm mother cells now divide into spermatids so that each spermatid has a single polar granule. This granule later enlarges into a band-shaped motor apparatus and becomes attached to one side of the nucleus. The nucleus also grows in size and becomes curved and later coiled into 2—3 coils. The motor apparatus bears numerous basal granules that give rise to the flagella of the spermatozoids (Fig. 11·21, A—E). The unused food, some plastids and cytoplasm form a broad posterior vesicle. The spermatozoids are liberated within thin membranous sheath which is discarded after liberation in water.

Archegonia

(*a*) **Structure** (Fig. 11·23, E, F). The structure and development of the archegonium is almost similar in all the leptosporangiate ferns. A mature archegonium of *Dryopteris* has a neck composed of four longitudinal rows of cells each row up to 5 cells in height. The neck is curved and bent away from the apical notch of the prothallus, *i.e*, towards the antheridia. The venter is embedded in the tissue of the prothallus (central cushion) and has no sterile jacket surrounding it. The tissue of the prothallus serves this purpose. The neck encloses a neck canal which is filled with a single, binucleate neck canal cell. The venter also encloses a cavity which contains a small ventral canal cell and a large egg or the female gamete. The neck canal cell, the ventral canal cell and the egg cell form an axial row of cells. The uppermost four cells of the archegonial neck act as the **cover cells.** Just before fertilisation the neck canal cell and the ventral canal cell disintegrate and become mucilaginous. On access of water this mucilage swells and exerts pressure on the topmost tier of neck cells (cover cells) which give way and make an open passage (Fig. 11·23, F). A drop of mucilage oozes out of the open neck.

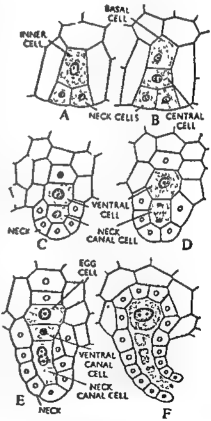


Fig. 11·23 (A—F). *Dryopteris.* **Various stages in the development of an archegonium.**

(*b*) **Development** (Fig. 11·23, A—F). The archegonium develops from a single superficial cell which

divides by a transverse wall into an upper smaller **primary cover cell** and a lower larger cell (*mother cell of the central cell*). The lower cell divides again by a transverse wall so that the young archegonium has a row of three cells, the upper *primary cover cell*, the middle **central cell** ar
The primary cover cell
quadrant of diagonally arr-
are the **primary neck cells**. Meanwhile the central cell has divided into an upper **primary neck canal cell** and a lower **primary ventral cell** (Fig. 11·23, C, D). The primary neck cells divide transeversely *to form a neck 3—5 or 7 cells in height (Fig. 11·23, C—E)* The neck canal cell grows in between the neck cells and forms a single neck canal cell whose nucleus divides into two (Fig. 11·23, D) so that it becomes binucleate (Fig. 11·23). The primary ventral cell divides transversely into an upper smaller **ventral canal cell** and a lower larger egg cell (Fig. 11.23, E). The neck becomes curved due to the unequal growth of its cells.

Fertilisation. It occurs in the presence of water between the surface of the prothallus and the soil. Since the sex organs are in direct contact with the film of water (due to their position) fertilisation presents no difficulties. If the young prothalli that bear only antheridia (due to the prothalli being protandrous) are growing in company with the older prothalli (that have both archegonia and *antheridia*), *the thin film of water surrounding them contains* numerous spermatozoids. Some of these are attracted by the *malic* ... from the mucilage exuded by the *open* ... Thus attracted they swim ... the neighbourhood of the ... some of them make their way down *the neck* ... *ly one of them is able to penetrate* ... *(Fig. 11.24, A)*. The male and the female nuclei fuse (*syngamy*) and form a diploid fusion *nucleus* surrounded by a cytoplasm of the egg, which secretes a wall around it and forms the **zygote** or the **oospore**. Becquerel (1931) reported that several archegonia on the same prothallus of *Dryopteris filix-mas may be fertilised and the zygotes of all of them may start* developing into embryos but only *one* is able to develop into a complete embryo. He even reported two sporophytes on the same prothallus. This is, however, very rare. After fertilisation the growth of the prothallus stops. The cells of the archegonial venter proliferate and form a cap like *calyptra* around *the fertilised egg*.

Embryogeny (Fig. 11·24). The zygote develops within the archegonial venter into a young embryo. The embryogeny of *Dryopteris filix-mas* was studied by Hofmeister (1865), Becquerel (1931), and *Vladesco (1935, 1937). Vladesco cultured* the prothalli of *D. filix-mas* on burnt soil and found that several embryos can develop on the same prothallus and even observed two embryos *in* one archegonium (1937). The zygote divides first by a wall parallel to the long axis of the archegonium. Two unequal cells are formed (Fig. 11·24, B). *The smaller cell, which is towards t*... x of the

prothallus is the epibasal cell and the larger is the hypobasal cell. The second wall is laid in a transverse plane and forms a quadrant

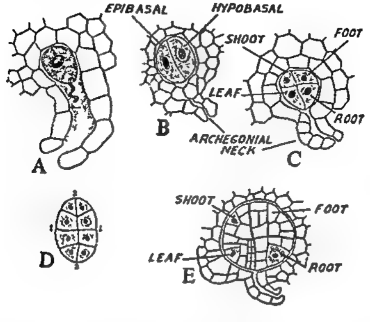


Fig. 11·24 (A—E). Early stages in the development of Embryo in *Dryopteris* sp. A. Archegonium with fertilised egg or the zygote; B. The zygote has divided into a two-celled embryo; C. Quadrant stage; D. Octant stage; E. Later stage showing apical cells of the primary organs. (Based on Vladesco, 1935)

stage (Fig. 11·24, C). The third wall is also transverse (perpendicular to long axis of archegonium) and results in the formation of an octant or eight-celled stage (Fig 11·24, D). Further divisions result in the formation of a 16-celled and 32-celled embryo. At the 32-celled stage the differentiation of the various organs of the young sporophyte may become evident (Fig. 11·24, E). The shoot arises from the anterior superior octants, the first leaf from anterior-inferior octants, the root from the posterior-inferior octants and the foot from posterior-superior octants (Fig. 11·24, E). The foot also occupies a portion of the anterior-superior octants and is well developed. The shoot and the leaf apices are not formed by the activity of three-sided apical cell but one of the larger cells in these segments gives rise to the respective apices of shoot and leaf (Vladesco, 1935). [illegible] quite early in develop-m[illegible] provascular tissue is e[illegible] t. This tissue develops into vascular strand and becomes adjoined with a vascular strand that develops below the shoot apex.

During further development the root grows rapidly and pierces through the calyptra to establish contact with the soil. Later the

At this stage the vasculature appears like the **dicyclic dictyostele** (Fig. 12·2). The peripheral ring of vascular bundles or the meristeles is separated from the medullary meristeles by an incomplete

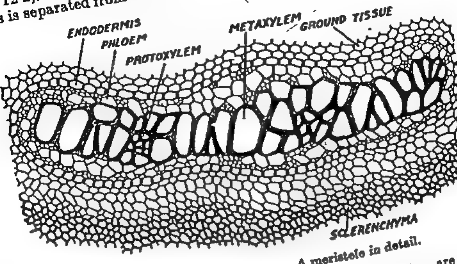


Fig. 12·3. *Pteridium aquilinum*. A meristele in detail.

patch of sclerenchyma. The meristeles of the outer ring are small and larger in number whereas there are only two or rarely more meristeles in the inner ring.

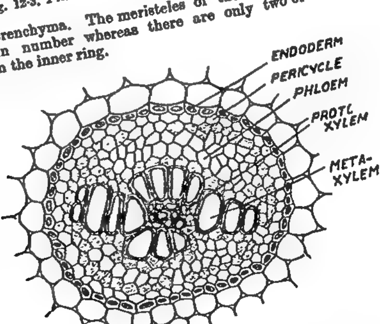


Fig. 12·4. *Pteridium aquilinum*.
A smaller meristele showing detailed internal structure.

Each meristele (Figs. 12·3 and 12·4) has an outer ring of the endodermis. The cells have casparian bands on their radial walls. Next to this is the pericycle. It may be composed of one or two layers of thin-walled cells surrounding the phloem. The phloem has an outer ring of smaller sieve elements and larger parenchyma

prothallus is the epibasal cell and the larger is the hypobasal cell. The second wall is laid in a transverse plane and forms a quadrant

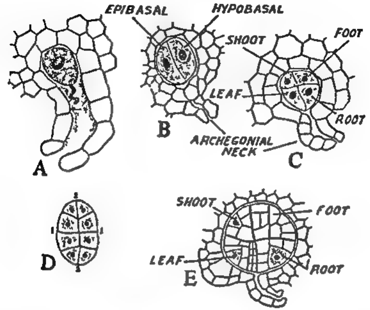


Fig 11·24 (A–E). Early stages in the development of Embryo in *Dryopteris* sp. A. Archegonium with fertilised egg or the zygote; B. The zygote has divided into a two-celled embryo; C. Quadrant stage; D. Octant stage; E. Later stage showing apical cells of the primary organs. (Based on Vladesco, 1935)

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During further development the root grows rapidly and pierces through the calyptra to establish contact with the soil. Later the

divides by a transverse wall into an upper smaller **primary cover cell** and a lower larger cell (mother cell of the central cell). The lower cell divides again *by a transverse wall so that* the young archegonium has a row of three cells, the upper primary cover cell, the middle **central cell** and the lowermost **basal cell** (Fig. 11·23, B). The primary cover cell divides by the intersecting walls into a quadrant of diagonally arranged four cells (Fig. 11·23, A, B). These are the **primary neck cells** Meanwhile the central cell has divided into an upper **primary neck canal cell** and a lower **primary ventral cell** (Fig. 11·23, C, D). The primary neck cells divide transeversely to form a neck 3—5 or 7 cells in height (Fig. 11·23, C—E) The neck canal cell grows in between the neck cells and forms a single neck canal cell whose nucleus divides into two (Fig. 11·23, D) so that it becomes binucleate (Fig. 11·23). The primary ventral cell divides transversely into an upper smaller **ventral canal cell** and a lower larger egg cell (Fig. 11.23, E). The neck becomes curved due to the unequal growth of its cells.

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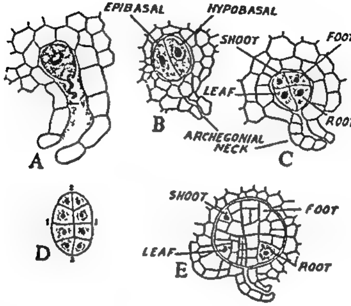

Fig. 11·24 (A—E). Early stages in the development of P... sp. A. Archegonium w... ded into a two-celled e... stage showing apical c...

stage (Fig. 11·24, C). The third wall is also transverse (perpendicular to long axis of ... and results in the formation of an ... 11·24, D). Further divisions result ... and 32-celled embryo. At the 32- ... of the various organs of the young sporophyte may become evident (Fig. 11·24, E). The shoot arises from the anterior superior octants, the first leaf from anterior-inferior octants, the root from the posterior-inferior octants and the foot from posterior-superior octants (Fig. 11·24, E). The foot also occupies a portion of the anterior-superior octants and is well developed. The shoot and the leaf apices are not formed by the activity of three-sided apical cell but one of the larger cells in these segments gives rise to the respective apices of shoot and leaf (Vladesco, 1935). The root apex originates quite early in develop- ... vascular tissue is ... his tissue deve- ... vascular strand ... below the shoot apex.

During further development the root grows rapidly and pierces through the calyptra to establish contact with the soil. Later the

first leaf emerges through the apical notch of prothallus. It turns green and starts photosynthesis. The shoot grows slowly

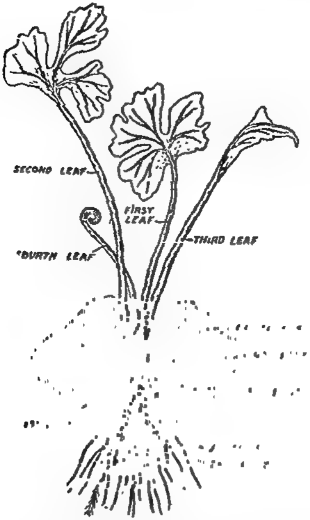

Fig. 11·25. Prothallus of *Dryopteris* bearing a young sporophyte with three leaves.

and becomes evident after the young sporophyte has produced a few young and juvenile leaves and primary roots (*Fig.* 11·25). The shoot grows underground and bears adventitious roots and young fronds.

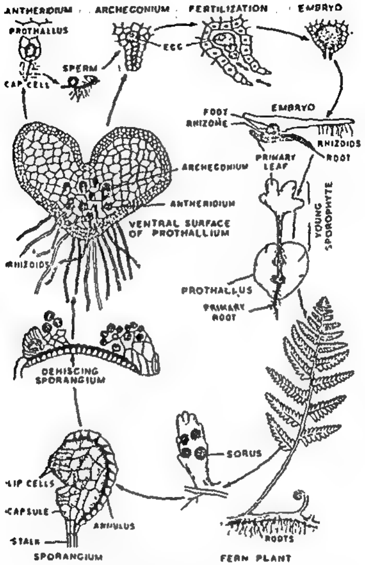

Fig. 11·26. A diagrammatic representation of the life cycle of a fern.

CHAPTER XII

Sub-Family PTERIDOIDFAE

This sub-family includes 12 genera and about 278 species and is characterised by the following features :—

1. Leaves are pinnate compound and may be unipinnate (*Pteris vittata*)

Fig. 12.1 (A—B). Portion of a sporophyte of *Pteridium aquilinum* showing habit (A).
B. A pinna showing position of sori.

or several times pinnate (*Pteridium*). Palmately compound in some cases, venation furcate and open or closed. In some cases venation is sparsely reticulate (*Lonchitis, Histiopteris*).

2. The sporangia occur in marginal or intramarginal sori. The sori are continuous, *i.e.*, coenosori, and are borne at the vein ends.

3. The sori are covered by the reflexed margins of the leaflets (false indusium). In some cases, *e g., Pteridium* and *Paesia* the sorus is also covered by a thin inner indusium. In *Lonchitis* the inner or lower indusium is replaced by hair. The sori may be gradate or mixed. The spores lack a *perispore*.

PTERIDIUM AQUILIDIUM (L. Kuhn)

It is widely distributed and a cosmopolitan monotypic genus that has several varieties and sub-species. It is widely distributed in India along entire Himalayan tract and grows well at altitudes between 1,000 and 3,000 metres. The species is found commonly on forest floors, edges of forests, exposed mountain slopes and on open grass lands. It is a very hardy plant and once established it does not permit other ferns to grow in the area and becomes an obnoxous field pest. It reaches its climax in the moist tropical regions, where it forms evergreen and permanent shrubby growth. It occurs almost all over the world except the arctic zone and the temperate South America.

SPOROPHYTE

Morphology

Rhizome. The rhizome is subterranean and grows 6 to 15 centimetres below the surface of the soil. The rhizome is long, creeping and profusely branched. Watt (1940) described the branching of the rhizome in *Pteridium aquilinum*. He distinguished three types of branches that arise from the sympodial rhizome. These are :—

1. *Long Shoots*. They arise from the parent axis and grow in the same direction thus penetrating deep in the soil. They have longer internodes and do not bear leaves.

2. *Intermediate Shoots*. After their origin from the parent axis they grow obliquely upwards for some distance and then run horizontally. They do not bear leaves.

3. *Short Shoots*. They also grow obliquely upwards and then run horizontally a little below (2—10 cm.) the soil surface. They bear leaves and have short internodes.

Branches of varying lengths that fall within the range of these three types have also been reported. The profusely branched rhizome presents a complicated system of branching and affords an efficient anchorage to the species. It is profusely covered with multicellular hair. The scales are absent.

The young plant has an unbranched creeping rhizome with 4—10 alternating leaves. It grows under the soil and soon bifurcates

dichotomously into two equal dichotomies. Each dichotomous branch bears a leaf near its point of origin from the main axis. Both these branches grow deep into the soil and bear leaves that are arranged in a spiral manner. The axis continues to branch dichotomously, but these dichotomies are unequal. The shorter branch bears a leaf. [illegible] rity, it looks like a bud [illegible] these branches as short [illegible] as perhaps regarded by him as a long shoot.

Leaves. The young plants bear leaves on the main axis but as the plants grow older the leaves seem to be restricted to the short and thick branches. The older portions of rhizome are beset with bases of old leaves and hair. They arise on the upper side of the rhizome and are borne in an alternate manner. They arise at an appreciable distance from each other and are circinately coiled when young. A mature leaf may vary in length from 2—12 feet. It is tripinnately compound and has a distinct petiole that is as long as the pinnately divided lamina. The portion of the petiole that extends into the lamina is called the rachis. The lower branches of the rachis are longer and gradually decrease in length towards the apex so as to give a deltoid or a conical appearance to the laminar portion (Fig. 12 1).

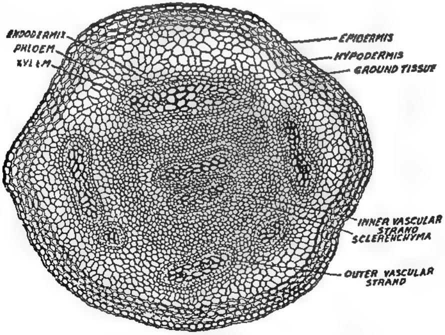

Fig. 12·2. A transverse section through mature rhizome of *Pteridium aquilinum* showing detailed internal structure.

The pinnules are traversed by a large and prominent mid-rib [illegible] which arise lateral veins. The veins run obliquely upwards [illegible] are furcate, *i.e.*, they branch dichotomously (*Fig. 12·1, B*). The

pinnules are firm and rough to touch (sub-coriaceous). The petioles are covered with unbranched and multicellular hair.

Roots. They arise at irregular intervals all along the ventral or lower surface of the rhizome and are sparingly branched. They are adventitious and endogenous in origin.

ANATOMY

Rhizome. Gottlieb (1959) studied the anatomy of the rhizome in *Pteridium aquilinum* right from the seedling stage and recognised six well marked stages in the ontogeny of the stele. These are :—

(*i*) *Protostelic stage.* A week-old stem that is hardly 6·8 mm. long and bears one or two young leaves has a single protostelic vasculature. The xylem forms a solid central core.

(*ii*) *Siphonostelic stage.* A five to-six-week old stem is almost upright and bears 2-5 leaves. It has siphonostelic vascular cylinder with only outer endodermis, pericycle and phloem (ectophloic siphonostele). This condition persists till the stem is about 2½ to 3 months old.

(*iii*) *Solenostelic stage.* As the young stem takes its course down into the soil and establishes itself as a rhizome the siphonostele is broken into two separate and unequal strands. The rhizome is about 5—10 mm. in length and is more than 2½ to 3 months old.

(*iv*) *Dictyostelic stage.* After the third stage when the rhizome has achieved a length of about 1·5—2·0 mm. the two larger or lower strands break up into a number of smaller strands or meristeles. They are arranged in a ring and some of them have a direct connection with the leaf traces and are formed due to the appearance of leaf gaps whereas others have no connection with the leaf or branch traces and appear due to 'stelar perforation'. At this stage the rhizome starts branching and bears a number of short shoots with leaves.

(*v*) *First Medullary Bundle Stage.* This stage starts when rhizome is about 6 cm. or more long and has achieved the age of 4 months. A medullary bundle originates from the inner side (towards pith) of one of the lower peripheral bundles. This bundle separates from the peripheral bundle and forms the first medullary bundle.

(*vi*) *Second Medullary Bundle Stage.* This stage starts when the rhizome is 6—12 months old and is up to 20 cms. long. A second medullary bundle arises from one of the lower peripheral bundles and separates from it as a second medullary bundle. This is the adult condition of the rhizome. This stage persists in older rhizomes and there is no further alteration in the stelar organisation.

At this stage the vasculature appears like the **dicyclic dictyostele** (Fig. 12·2). The peripheral ring of vascular bundles or the meristeles is separated from the medullary meristeles by an incomplete

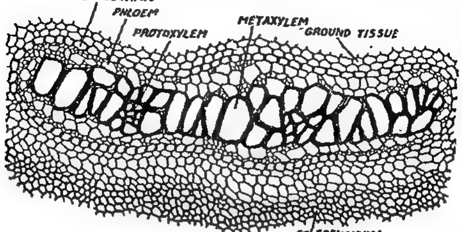

Fig. 12·3. *Pteridium aquilinum*. A meristele in detail.

patch of sclerenchyma. The meristeles of the outer ring are small and larger in number whereas there are only two or rarely more meristeles in the inner ring.

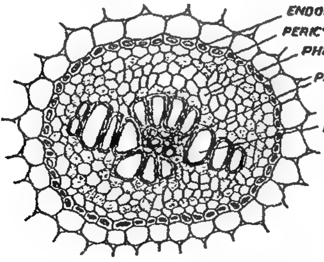

Fig. 12·4. *Pteridium aquilinum*.
A smaller meristele showing detailed internal structure.

Each meristele (Figs. 12·3 and 12·4) has an outer ring of the endodermis. The cells have casparian bands on *their radial walls*. Next to this is the pericycle. It may be composed of one or two layers of thin-walled cells surrounding the phloem. The phloem as an outer ring of smaller sieve elements and larger parenchyma

cells that constitute the **protophloem** and an inner ring of larger sieve elements or the **metaphloem.** The phloem has no companion cells and phloem fibres and almost completely surrounds the mesarch xylem (12·4). The phloem and xylem elements resemble those of *Dryopteris* in their structure and arrangement.

The entire stelar region is embedded in the parenchymatous ground tissue which is surrounded by the sclerenchymatous hypodermis, which forms the peripheral strengthening tissue (Fig. 12·2). It is encircled by the outermost layer of thin-walled or thick-walled cells called the epidermis. The outer walls of the epidermis are cutinised.

ROOT

The structure of the root resembles that of *Dryopteris* in all its details. It is diarch (Fig. 12·6, C).

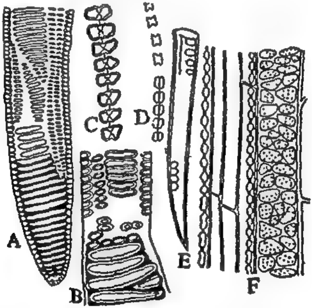

Fig. 12·5. Vascular elements of *Pteridium aquilinum*.
A. A portion of tracheid showing scalariform pits.
B. Enlarged portion of A.
C. L.S. portion of lateral wall of a tracheid showing pits.
D. L.S. through oblique wall of a tracheid showing pits without closing membranes.
E. A portion of a sieve tube separated by maceration.
F. L.S. through a meristele showing phloem region with a sieve tube and parenchyma cells.
(A—D, after De-Bary; E—F, after Bower).

(*i*) **Pinnule** (Fig. 12·6, B). A T.S. through the pinnule reveals that the internal structure is similar to that of a bifacial leaf. There ... rith stomata restricted to the ... ween the two epidermal layers ... distinguishable into palisade

parenchyma and the spongy parenchyma. The former forms a layer or more of columnar cells arranged below the upper epidermis. The cells of this layer contain abundant chloroplasts. The spongy zone is made up of numerous loosely arranged and lobed parenchymatous cells. They enclose small and large intercellular spaces and contain chloroplasts The palisade is absent in region of the veins where the cells are compactly arranged so as to give strength to this region.

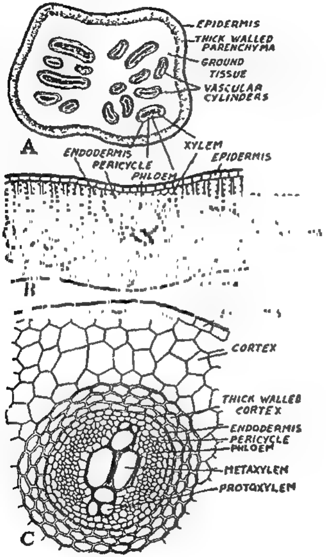

Fig. 12-6. *Pteridium aquilinum*.
A. T.S. through petiole (diagrammatic) showing internal structure.
B. V.S. pinnule. C. T.S. root.

... almost spherical in shape and each ... endodermal layer. It may

(*ii*) **Petiole** (Fig. 12·6, A). A transverse section of the petiole of a young plant shows an outer epidermal layer encircling a few layered thick, sclerenchymatous hypodermis, which in turn encircles the parenchymatous ground tissue. Embedded in the ground tissue are the meristeles or the leaf traces. The number of leaf traces ... of the leaf. The larger petioles have ... ler petioles ... arranged ... ke that of the meristele.

The pattern of apical growth is similar to that of *Dryopteris.*

Vegetative Propagation

Pteridium propagates extensively by vegetative means. The older parts of the rhizome decay. The process of decay continues

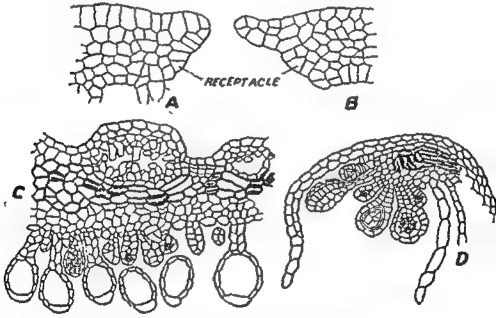

Fig. 12·7 (A—D). *Pteridium aquilinum.* Development of receptacle and the sorus.
A. B. Vertical sections through young sporophylls show- ...
C. ... mixed
D. ... e flaps.
(After Bower)

and when it reaches the branching region, the branches separate and act as independent and separate plants. This is the only method prevalent in *Pteridium* and leads to a gregarious habit.

Sporophylls and Sori. Every leaf in *Pteridium* is a potential sporophyll as there is no segregation of reproductive and vegetative

eaves. The ultimate segments of the lamina or the *pinnules* bear porangia on their margins. The sporangia develop on marginal eceptacles (Fig 12·1, B) and are grouped in a continuous or a conluent and a linear type of sorus. It is also called **a coenosorus**. As a matter of fact numerous smaller sori occur so close to each other that they lose their identity and appear as one long sorus disposed along the two lateral margins of the fertile pinnules. A vertical section of the sorus (Fig. 12·7, A—D) reveals that the receptacle is traversed by a vascular strand that runs underneath the sporangia and connects the free ends of the veins. The sorus is protected by two flaps that grow a little to cover the sporangia from the lower end. The upper indusial flap (Fig. 12·7) is formed by the reflexed margin of the pinnule and is well developed. The lower indusial flap is a true indusium whereas the upper flap is a false indusium because it is simply a revolute margin of the pinnule and not a specially developed structure. The lower or the true indusium is not well developed and is a thin sheet of tissue made up of a single layer of thin walled cells.

The receptacle originates from a row of wedge shaped initials that occupy the margin of the pinnules (Fig. 12·7. A, B). These initials divide and redivide to form a continuous receptacle which bears sporangia. The adaxial or the upper indusium appears as a superficial outgrowth from the marginal segments of the leaf a little above the receptacular initials. It soon overgrows and envelops the developing receptacle. The lower indusium arises late and is comparatively less developed. The sequence of sporangial development appears to be basipetalous in a young sorus but it soon changes to a mixed type. In some varieties the order of development remains basipetalous (*P. aquilinum* var. *caudatum*), and the sorus is gradate.

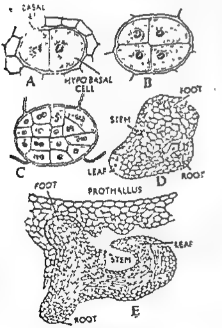

Fig. 12·8. *Pteridium aquilinum* (A—E). Various stages in the development of embryo.

Sporangium. Structure, development and mode of dehiscence of the sporangium are similar to that of *Dryopteris*. The number of spores produced per sporangium is also 48. Manton (1950) reported the haploid chromosome number as $n=52$.

Gametophyte. The spores are tetrahedral and lack perispore. ... and the structure of prothallus is similar ... structure and development of

The development of the zygote and the details of segmentation pattern leading to the formation of a mature embryo and then to the young sporophyt[illegible] similar to the other [illegible] Chapter 8 and also

PTERIS Linn

It is another widely distributed genus of this sub-family. It is represented by about 250 species that grow abundantly in the

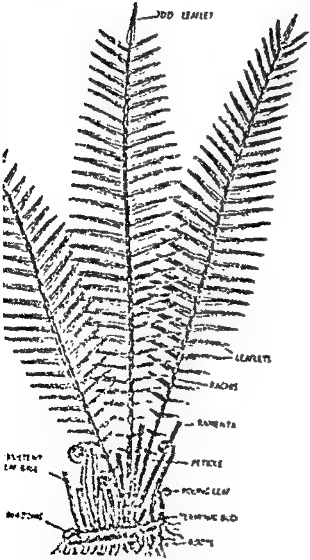

Fig. 12.9. A complete plant of *Pteris vittata*

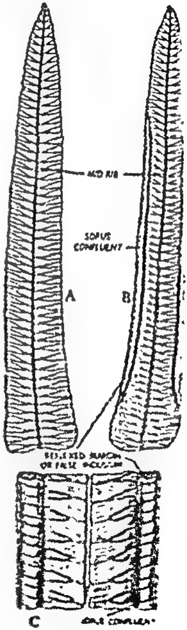

Fig. 12.10. *Pteris vittata*
A. a sterile pinna,
B. a fertile pinna ab[illegible] sorus.
C. portion of B

tropical and sub-tropical regions of the world. The common species in India are *Pteris vittata*, *Pteris cretica L.*, *Pteris biaurita L.*, *P. quadriaurita Retz.*, *P. stenophylla Wall.*, and *P. Wallichiana*. *Pteris vittata* is a low level fern and brings out new leaves throughout the year. It is very common along mountain walls and grows up to 1,200 metres above sea level. *P. quadriaurita* grows abundantly along road-sides and the valleys throughout the North Western and Western Himalayas. *Pteris cretica* grows well from 1,200—2,400 metres above sea level.

The plants have creeping rhizomes in *P. biaurita*, *P. vittata* (Fig. 12·9) and *P. grandiflora*. In *P. cretica* the rhizome is branched short, stumpy and semi-erect. The rhizome is covered with scales. Hair are absent. Roots arise from the lower surface of the rhizome or they may arise all over the surface as in *P. biaurita*.

The leaves are pinnately compound (Fig. 12·9) rarely digitate. The petioles are covered with scales. Venation is of open furcate

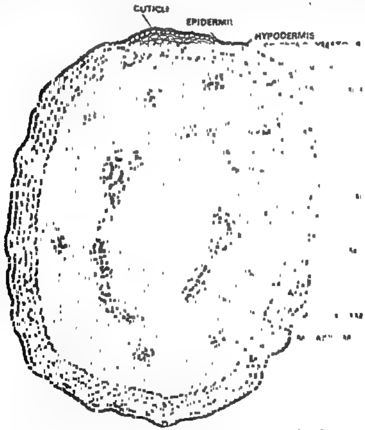

Fig. 12·11. T.S. rhizome of *Pteris vittata* showing dicyclic dictyostele.

type (Fig. 12·10). The leaves in *P. vittata* are once pinnate (Fig. 12·9). The pinnae are smaller near the base, larger near the

middle and again go on decreasing in length towards the apex so as to give a spindle like appearance to the frond. Leaf apex is

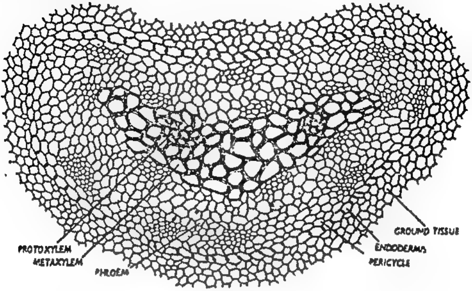

Fig. 12·12. A meristele from the rhizome of *Pteris vittata* showing detailed internal structure.

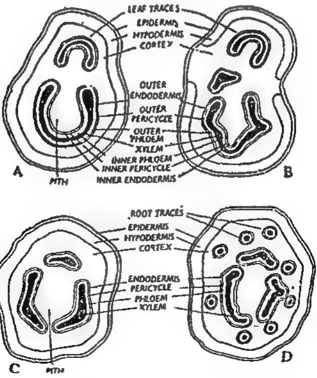

Fig. 12·13. *Pteris vittata.* Cross-sections of various levels showing changes in stelar

occupied by an odd leaflet or pinna. Venation in this case is open furcate. Every pinna is traversed by a central midrib which gives off lateral veins that bifurcate near the tip. The pinnae are sessile and are broad at the base and gradually larger towards the apex (Fig. 12·9). The leaves are bipinnate in *P. biaurita*. The leaflets or pinnules are coriaceous or rough to touch.

Anatomy. The stelar organisation of rhizome varies with species and sometimes in the same species. It is solenostelic in *P. grandiflora* and *P. vittata*, a simple dictyostele in *P. cretica* and younger regions of *P. vittata* In the younger branches of the rhizome in *P. biaurita* the stele is a mixed protostele in the lower region. It becomes siphonostelic a little higher up and solenostelic near the apex. In the main rhizome dictyostelic condition is also found. The same is the case in *P. palmata* willd (Chandler, 1905). In *P. vittata* the stelar organisation (Fig. 12·11) changes to a dicyclic dictyostele in the apical regions of the rhizome. This condition is achieved by the separation of small circular or oval strands or root traces from the outer surface of the parent meristeles that in turn were derived by the stelar perforation of the solenostelic arc. These changes lead to the formation of irregularly arranged root traces around 4—5 large meristeles (Fig. 12·11). There are no medullary strands.

The pinnule has upper and lower epidermal layers (Fig. 12·14). In *P. cretica* the upper epidermis has larger cells with less sinuous

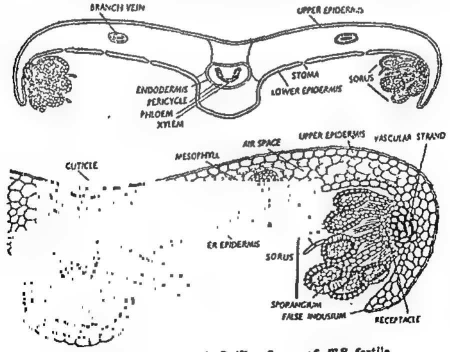

Fig. 12·14. *Pteris vittata*. A. Outline figure of T.S. fertile leaflet showing internal structure, false indusium and sporangia borne on receptacle. B. Portion of A in detail.

walls. The stomata are restricted to the lower epidermis which has smaller cells and more sinuous walls. The mesophyll may or may not be differentiated into palisade parenchyma and spongy parenchyma. The midrib region has single concentric type of vascular strand (*P. vittata*) with distinct endodermis. The bundle sheath extensions are prominent and occur as groups of thick walled cells below the upper and above the lower epidermis. Palisade and spongy tissue is absent around the mid-rib.

The petiole (Fig. 12·15) is traversed by a single C-shaped (*P. vittata*) or U-shaped or V-shaped leaf trace. In *P. biaurita* the U-shaped leaf trace enters the petiole and becomes V-shaped higher up. The xylem has two adaxial hooks. In the rachis the petiole trace gives off strands into its pinnae if the leaf is unipinnate or it divides to give rise to secondary and tertiary pinna traces in bipinnate leaves (*P. biaurita*). The rachis traces are marginal in origin and are *usually flat U-shaped or shallow arc-like*. In *P. cretica* the C-shaped leaf trace divides into two strands which unite into a single V-shaped strand higher up in the petiole. The hooked

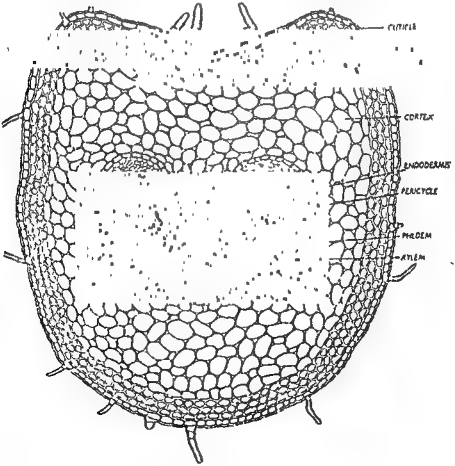

Fig. 12·15. T.S. of Petiole of *Pteris vittata*.

xylem of the leaf trace, the marginal origin of the pinna and rachis traces and the solenostelic tendency in the stem stele are the primitive features of the genus. The root is diarch.

The sorus is of the continuous type (coenosorus) as in *Pteridium*; but is protected only by the upper indusial flap that is formed by the inturned or reflexed margins of the pinnae (Fig. 12·15). The receptacle is intramarginal in origin. The lower or the true indusium is absent. The lower or ventral surfaces of the leaves in *Pteris biaurita* bear multicellular and linear hair. The ramenta in *P. cretica* bear glandular hair (Singh, 1963). The sporangia are mixed. The structure (*Fig.* 12·16) and development of sporangia is similar to that of *Dryopteris* Each sporangium produces 48 spores.

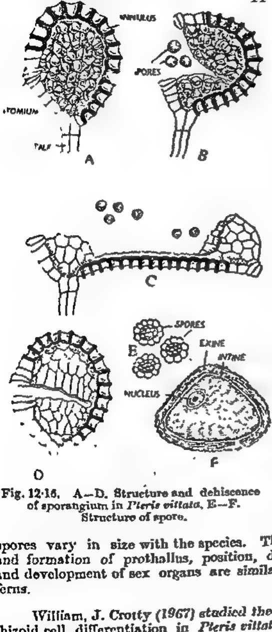

Fig. 12·16. A—D. Structure and dehiscence of sporangium in *Pteris vittata*, E—F. Structure of spore.

The spores (Fig. 12·16) are bluntly or roughly triangular and have a distinct triradiate mark. The spore wall is thick and has an outer exine and an *inner intine*. The former may be variously sculptured. In *P. biaurita* it bears many irregular bands of thickening (Singh, 1963). In *P. cretica* the exine has *variously bent bands of* thickening material. The spores vary in size with the species. The germination of the spore and formation of prothallus, position, distribution and structure and development of sex organs are similar to other polypodiaceous ferns.

William, J. Crotty (1967) *studied the germination of spore and rhizoid cell differentiation in Pteris vittata L.*, under experimental conditions. The exine ruptures and the uninucleate contents come out and grow into a small cylindrical thallus cell (Fig. 12·11). A unicellular rhizoid arises from the thallus cell and grows into long and tubular, primary rhizoid (Fig. 12·17, C) The thallus cell

transversely to form a short filament of green cells (Fig. 12·17, B). One or more of the terminal cells of this filament divide by longitudinal walls to form a plate of cells (Fig. 12·17, B). Further divisions, transverse and vertical, lead to the formation of a bigger plate one layer of cells in thickness. Later a row of marginal meristematic cells is distinguished and an apical notch is formed due to greater growth of cells on the sides (Fig 12·17, A). Divisions are mainly restricted to the region of the notch, region behind the notch and in the lateral wings. The cells behind the apical notch divide along two more planes and form a thick central cushion. The secondary rhizoids arise from the posterior regions of the prothallus. Recently mature thallus cells act as rhizoid mother cells. At this stage, according to Crotty (1967) the prothallus has two types of cells : (*i*) the thallus cells which do not stain with pyronin-methyl green and remain living an hour after the staining process, (*ii*) the rhizoidal cells, which readily stain with pyronin-methyl green The stain kills the cell cytoplasm.

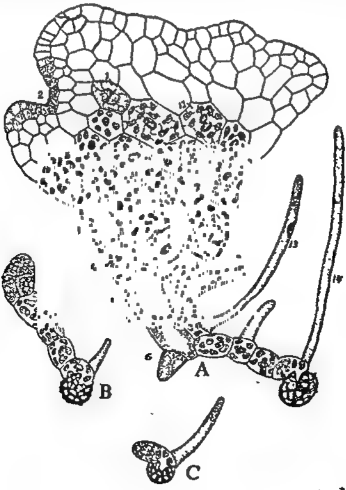

Fig. 12·17 (A—C). *Pteris vittata*. Stages in the germination of spore and formation of rhizoid cell (After Crotty William, 1967).

Differentiation of rhizoid cells. The thallus cell in which the rhizoid cell will differentiate shows the following stages :—

(i) The nucleus and the nucleoli enlarge considerably. A delicate network of cytoplasmic strands that stain red with pyronin-methyl green appear around the nucleus (Fig. 12·17, A, 11). The networks extends considerably beyond the nucleus periphery. The nucleus is in prophase stage. The appearance of this network of cytoplasmic strands around the nucleus is designated as the *corona stage* by Crotty (Fig. 12·17, A, 10).

(ii) The coronal network diffuses throughtout the cytoplasm and is not as prominent as before. A dense deposit of cytoplasmic

prophase nucleus is designated as the **perinuclear stage** (Fig. 12·17, A, 11).

(*iii*) The nucleus divides into two daughter nuclei. One is called the rhizoid cell nucleus and the other as nucleus of the remaining thallus cell (Fig. 12·17, A, 1). A wall is formed between [illegible] ·17, A,9). As a result a small lenticular [illegible] is differentiated from the large cell. So [illegible] segmented (Fig. 12·17, A-5). A few chloroplasts can also be seen in rhizoidal cell. Such chloroplasts lose their colour and only a few plastid like bodies remain in the rhizoid cell. This is the early stage of the internally segmented rhizoid cell.

(*iv*) The nucleus of the rhizoid cell is surrounded by a number of darkly stained (pyronin stained) cytoplasmic strands that radiate from all around the nucleus towards the periphery of cell Thus gives a wheel-shaped appearance (Fig. 12·17, A, 8) and this stage is, therefore, called *"wheel stage"*.

(*v*) The rhizoid cell starts protruding out (Fig. 12·17, A, 6-7), the strongly pyronin-stained material of the wheel-stage increases in concentration and the strands become more prominent. The growth of the rhizoid wall is restricted to the apical region. As the rhizoid elongates the darkly staining material and the nucleus move to the tip (Fig. 12·17, A-13). In the mature rhizoid (Fig. 12·17, A-14) the densely staining material at the tip disappears.

The structure and development of sex organs is similar to *Dryopteris*. The embryo development also resembles *Dryopteris in* general Fig. 12·18.

It includes about 50 species. A few species have been included under the genus *Phymatodes*. In India it occurs commonly as an epiphyte on tree trunks and branches. The common Himalayan epiphytic species are *P. microrhizoma*, *P. amoenum*, *P. subamoenum*, *P. steewartii*, *P. lachnopus*, and *P. lineare*. They grow on tree trunks or branches of *Quercus*, *Cedrus*, *Abies*, *Rhododendron* and rarely *Pinus wallichiana*.

Morphology. The rhizome is generally creeping (Fig. 13 1) and branched, sometimes fleshy semierect and glaucous The rhizome is covered with peltate, lanceolate and brownish scales or ramenta. The leaves may be simple and spathulate (*P. lineare*) or simple or deeply incised and pinnate. Venation may be free and furcate or reticulate and anastomosing. The older portions of the rhizome are covered with bases of old leaves. The younger leaves are circinately coiled. The leaf lamina is covered with multicellular hair. The stem is also clothed with multicellular hair that arise from the epider-

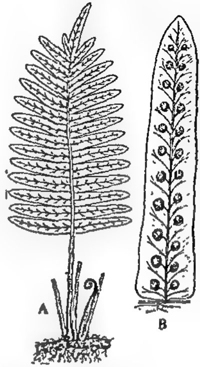

Fig. 13 1. *Polypodium* sp. A. Portion of a plant showing habit, B. A pinna-bearing sori.

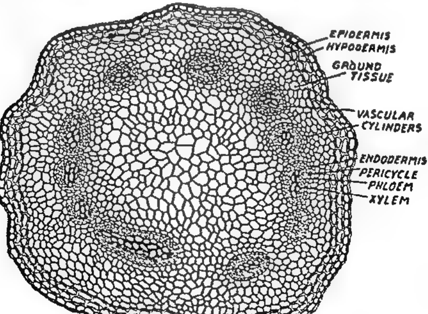

Fig. 13 2. *Polypodium*. T.S. rhizome showing detailed internal structure.

CHAPTER XIII

Sub-Families POLYPODIOIDEAE AND GYMNO-GRAMMEOIDEAE

SUB-FAMILY Polypodioideae

It is the ... species (C ... regions. ... Flora. Th ...

... Thunbg; *Phymatodes oxyloba* (Wall) Ching, *P. stracheyi* Ching, *P. ebenipes* (Hook) Ching, *P. malcadon* (Hook) Ching; *Drynaria mollis* Bedd.; *Loxogramme involuta* Wall. and *Microsorium membranaceum* (Den.) Ching.

The sporophytes have creeping or semi-erect and branched or sparingly branched subterranean rhizomes. The leaves may be simple or pinnate compound. Venation may be free or reticulate. The sori arise on the ventral surface of the sporophylls and are as a rule naked (exindusiate) and globose ...

... development.

POLYPODIUM L.

It is widely distributed and a common genus that occurs along the tropical and subtropical regions of the world. A few species are, however, found in the northern temperate regions (*P. vulgare*).

It includes about 50 species. A few species have been included under the genus *Phymatodes*. In India it occurs commonly as an epiphyte on tree trunks and branches. The common Himalayan epiphytic species are *P. microrhizoma*, *P. amoenum*, *P. subamoenum*, *P. steewartii*, *P. lachnopus*, and *P. lineare*. They grow on tree trunks or branches of *Quercus*, *Cedrus*, *Abies*, *Rhododendron* and rarely *Pinus wallichiana*.

Morphology. The rhizome is generally creeping (Fig. 13·1) and branched; sometimes fleshy semierect and glaucous. The rhizome is covered with peltate, lanceolate and brownish scales or ramenta. The leaves may be simple and spathulate (*P. lineare*) or simple or deeply incised and pinnate. Venation may be free and furcate or reticulate and anastomosing. The older portions of the rhizome are covered with bases of old leaves. The younger leaves are circinately coiled. The leaf lamina is covered with multicellular hair. The stem is also clothed with multicellular hair that arise from the epider-

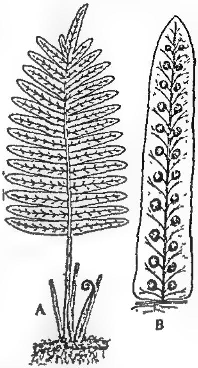

Fig. 13·1. *Polypodium* sp. A. Portion of a plant showing habit, B. A pinna-bearing sori.

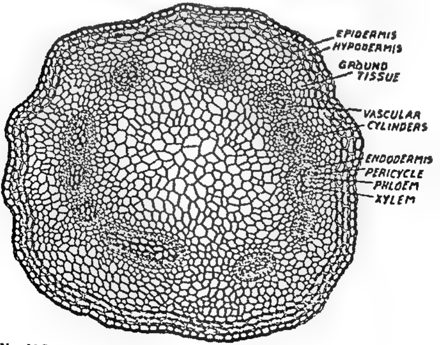

Fig. 13·2. *Polypodium*. T.S. rhizome showing detailed internal structure.

-mis. The adventitious roots are in large numbers and are branched. The roots originate endogenously and come out on the lower side of the rhizome.

Anatomy. The anatomy of the rhizome (Fig. 13·2), root and the sterile lamina is similar to that of *Dryopteris*. The stomata in the leaves are restricted to the lower epidermis and are irregularly distributed. In *P. lineare* Thunbg, *P. scouleri* Hook. et Grew. and *P. vulgare* Rehfus., the stomata are globular and are present even on the veins. The leaf epidermis is covered with club-shaped and multicellular hair in *P. lineare* (Singh, 1963). Non club-shaped hair occur around the mid-rib. The leaf mesophyll is not distinguished into palisade and spongy parenchyma and is, therefore, homogeneous. Rarely there is a slight differentiation.

The roots are diarch.

Vegetative propagation takes place by the death and the decay of the older portions of the rhizome thus setting free the branches that grow as independent plants.

REPRODUCTION

(a) Sporophylls and Sori. There is no distinction between sterile and fertile leaves. The sori arise on the ventral surface of

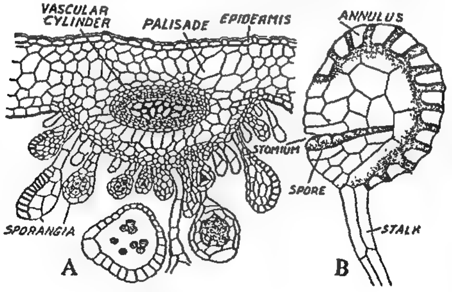

Fig. 13·3 (A—B). *Polypodium* sp.
A. V.S. through sorus. There is no indusium.
B. A sporangium.

13·1 B) or the fertile leaf and are borne at the single row on either side of usually spherical and may be small or large in size and are not protected by any indusium

(Fig. 13·3, A). The sori have a distinct receptacle that bears mixed sporangia. The sporangia may be mixed with hair or peltate scales, (*P. lineare*) and offer protection to the exindusiate sorus.

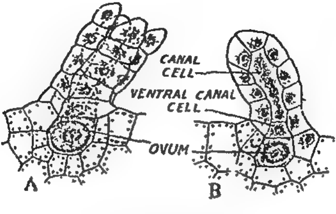

Fig. 13·4 (A—B). *Polypodium vulgare.*
A. Closed and mature archegonium.
B. Archegonium with open neck.
(After Strasburger)

(*b*) **Sporangia.** The structure (Fig. 13.3, B) and development (Fig. 13·3, A and 8.38) of the sporangium is leptosporangiate type and is exactly similar to that of *Dryopteris.* Each sporangium produces 48, dark brown big, elliptic (*P. lineare, P. vulgare, P. pteropus*) with flattened one side and thin walled spores. The size of the spore is usually ·057 × ·041 μ in *P. lineare* (Singh, 1963).

Gametophyte. The development and structure of prothallus and sex organs is exactly similar to that of *Dryopteris.*

The developnent of embryo and formation of embryo is also identical to other polypodiaceous ferns.

Sub-Family Gymnogrammeoideae

The sub-family includes about 27 genera that are of varied habits and habitats and possess uncertain interrelationships. Some of them come quite [illegible] usually terrestrial except for [illegible] plants vary in their height [illegible] to a few feet. The rhizome [illegible] branched. It is covered with scales or ramenta. The leaves are arranged spirally or alternate and may be simple, or compound. In *Craspedodictyum* Copeland and *Bommeria* Fournier, the leaves are palmately compound. In *Syngramma* J. Smith, the leaves are simple, lancolate or ovate with the free ends of the furcate veins united by a continuous, intramarginal veins. In *Adiantum, Coniogramma, Pityrogramma* and *Cheilanthes*, the leaves are pinnately compound and may be uni-, bi- [illegible] lecompound. The sori [illegible] nd are superficial, with [illegible] *liantum, Pellaea*). The [illegible]). somtimes confluer[illegible]terrupted sori that are [illegible] the connecting

commissure is present. Such a commissure is a single intramarginal vein that connects the free vein endings. This vein passes through receptacle of the sorus. *Ceratopteris* is an interesting member of this family (some include it in a separate family called Parkeriaceae) in which the sporangia occur singly at the vein ends and are spherical and subsessile. The fronds are dimorphic. In *Aspleniopsis*, *Syngramma*, *Coniogramma* the sporangia are mixed with paraphyses. Paraphyses are absent in other genera, e.g., *Gymnopteris*. Linear and oblong sori that occur along the veins are also known in some, e.g., *Pterozonium* Fee, *Coniogramme* Fee. Sporangia have a mixed arrangement on the receptacle and are shortly stalked or sessile. The spores are tetrahedral and globose. They lack perispore. The gametophytes and sex organs are similar in development and structure to other polypodiaceae.

The stem anatomy shows variations and may be siphonostelic, solenostelic or even dictyostelic. In *Adiantum* all the three types of steles are found at various levels on the same stem.

Some of them are epiphytic, a large number grow under moist and shaded localities and a few are xerophytic and grow on exposed places, e.g., *Cheilanthes albomarginata*. *Ceratopteris* is aquatic.

Fig. 18·5. *Adiantum capillus—veneris*. A complete plant showing external form.

Christensen (1938) divided the sub-family in 5 tribes A brief information about *Adiantum* L., which belongs to the tribe Adianteae is given here.

ADIANTUM L.

It is a widely distributed genus with about 200 species that grow abundantly in the tro[illegible] regions of the world and love moist and [illegible] ecies [illegible] atum [illegible] *lunu-* [illegible] species occur [illegible] part of the

fern flora. Nayar (1961) studied the morphology of 24 Indian species of *Adiantum*.

MORPHOLOGY

Rhizome. The rhizome in the genus *Adiantum* is covered with paleae and may be erect, *e.g., A. caudatum, A. edgeworthii* and *A. philippense*, or semi erect *e.g. A. pedatum*, or creeping as in *A. capillus-veneris* (Fig. 13·5), *A. thalictroides, A. pectinatum, A. peruvianum*, etc. The rhizome is hard and brown in the erect and semierect species and light brown and soft in the creeping forms. The paleae covering the rhizome vary in their shape or outline. They may be lanceolate (*A. pedatum* and *A. philippense*) to ovate lanceolate (*A. venustum; A. caudatum*) The paleae are attached to the rhizome by a short and broad stalk (Fig. 13·6). The base of the paleae may be variously auricled on either side of the stalk. The apex of the paleae is usually long and drawn out (Fig. 13·6). Its margin may be smooth (*A. capillus-veneris, A. venustum*) or dentate (*A. pectinatum*). The paleae develop as unicellular outgrowths which undergo transverse division to form a 5—10 cells high uniseriate hair (Fig. 13·6, I). The cells of this hair are longer towards the apex. The cells at the base of this hair divide longitudinally thus making it flat and multiseriate. Soon it assumes a lanceolate appearence. The basal cell develops into a short stalk (Fig. 13·6).

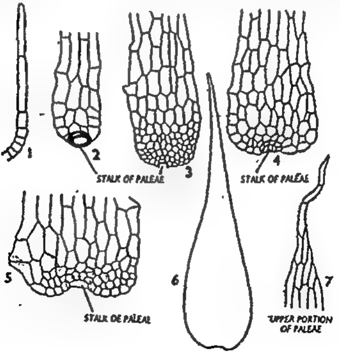

Fig 13 6. *Adiantum*,
The structure and development of paleae in *A. capillus-veneris*
(After Nayar, 1961)

Leaf. *Adiantum* has characteristic leaves that are, as usual, circinately coiled in the bud condition. The leaf has a dark brown to black and shining petiole which is traversed by a median groove devoid of the marginal ridges, on the adaxial side. The petiole is covered with paleae that may extend into the rachis and the leaflets (pinnae) as in *A. caudatum*. In some species the paleae are restricted to the base of the petiole only. Nayar (1961) has reported the presence of multicellular nonglandular hair all over the petiole and the rachis in some species. In some species such hairs are restricted to the adaxial groove. The base of the petiole is continuous with the cortex of the rhizome (Ching, 1957; Nayar, 1961). The petiole and the rachis are hard in all the 24 species found in India.

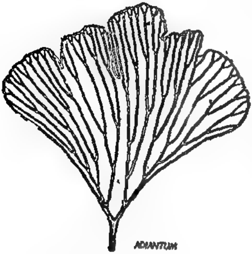

Fig. 13·7. A pinnule of *A. capillus veneris* showing venation.

The leaves may be once pinnate, *e.g.*, *A. caudatum*, *A. edgeworthii* and *A. philippense*; two to more pinnate in *A. capillus-veneris* (Fig. 13·5), *A. thalictroides*, *A. pectinatum*, *A. pedatum* and *others*. In *A. caudatum* the unipinnate leaves bear pinnae in alternate manner on either side of the strong rachis. The pinnae are stalked. The rachis may terminate in a pinna or may be elongated bearing a vegetative bud at the tip. Under favourable conditions this vegetative bud may develop into a daughter plant (when the leaf tip touches the ground) which in turn may repeat the process thus leading to a well known 'walking habit'. In the bi- or- tripinnate species the leaflets are called the pinnules. In *A. pedatum* the petiole forks at the tip forming a pair of diverging rachises. Each of these two rachises further branches on the side facing each other. These branches bear terminal and lateral

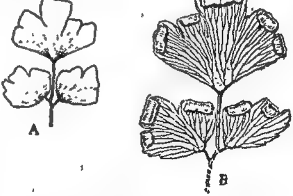

Fig. 13 8 (A—B). *Adiantum capillus-veneris*
A. Sterile pinnules.
B. Fertile pinnules as seen from ventral side.

pinnules. In *A. capillus-veneris* the rachis divides pinnately and the ultimate branches bear pinnules in an alternate manner. Each branch terminates in a pinnule. The terminal pinnule usually differs in shape and size from the lateral pinnules. The venation is free and dichotomous in all species (Fig. 13·7). The veins spread in a fan like manner in the lamina.

Root. The roots are adventitious and arise in clusters from the underside of the rhizome, in the creeping forms (Fig. 13·5) and from the base of the rhizome in the erect forms. They are black and wiry structures and are branched.

ANATOMY

A. **Rhizome.** (Figs. 13·9—13·11). In a transverse section the rhizome presents an irregular or wavy outline. It shows the following tissue systems :—

Epidermis. It forms the outermost layer of thin-walled or slightly thick walled cells. The cells are generally smaller in size and possess brownish walls. Externally the epidermal layer is lined with a thick cuticle.

Cortex or Ground Tissue. Next to the epidermis lies the extensive ground tissue that may be wholly parenchymatous or partly parenchymatous and partly sclerenchymatous. In some species (*A. peruvianum. A trapeziforme, A. pectinatum*) scattered groups of sclerenchymatous cells occur in the ground tissue. In *A. pedatum* and *A. caudatum* there is a distinct sclerenchymatous hypodermis below the epidermis. Next to it is the parenchymatous ground tissue whose cells may be small or large and enclose small intercellular spaces. In some species the entire ground tissue is composed of small parenchymatous cells with brown walls and there is no well defined sclerenchyma.

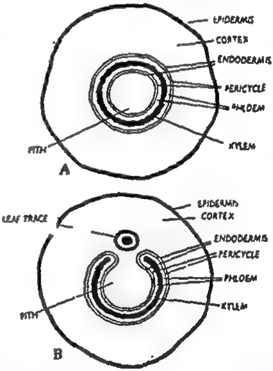

Fig. 13·9.
A. T.S. outline diagram of rhizome of *A. rubellum* showing siphonostelic organization.
B. T. S. rhizome (outline diagram) of *A. pedatum* showing solenostele.

Stele. The stelar organisation in *Adiantum* varies in the species of *Adiantum*. Nayar (1961) studied the anatomy of 24

species of *Adiantum* and gave a vivid description of the variations in the stelar system of the rhizome.

In *Adiantum rubellum* the stelar cylinder is **amphiphloic siphonostelic** (Fig. 13·9) at certain regions, *i.e.*, there is a complete and uninterrupted stelar cylinder with outer endodermis enclosing outer pericycle, outer phloem, xylem, inner phloem, inner pericycle and inner endodermis. In the centre there is a pith. At places where the **leaf trace** departs a **leaf gap** is left behind and the intact siphonostelic cylinder is broken at one point thus changing to a **solenostele** (Fig. 13·9, B). In *A. pedatum*, *A. flabellulatum*, *A. hispidulum*, *A. venustum*, *A. nobile*, *A. pectinatum* and many others the stelar cylinder is solenostelic.

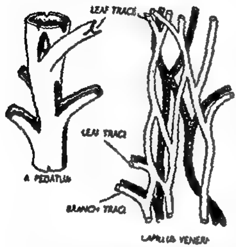

Fig. 13·10. Stereodiagrams of the Stelar organization in *A. pedatum* and *A. capillus-veneris* (After Nayar)

In *A. capillus-veneris* (Fig. 13·11), *A. thalictroides*, *A. caudatum*, *A. edgeworthii* and *A. philippense* the stelar cylinder is *dictyostelic*. It is dissected by many closely placed and overlapping leaf

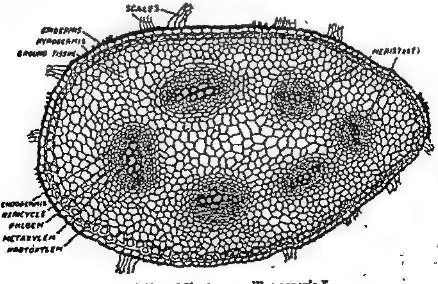

Fig. 13·11. *Adiantum capillus-veneris L.*
T.S. rhizome showing a dictyostele with six meristeles.

gaps arranged in one or more close spirals. In *A. capillus-veneris* the stelar cylinder in the young plants is **solenostelic** because the leaf gaps or lacunae are small. In the older plants the gaps expand

excessively and cut the stelar cylinder into a reticulum with long meshes (Nayar, 1962).

The root traces arise indiscriminately from the outer surface of the stelar cylinder and have no connection with the leaves or branches. They are diarch and acquire a sclerenchymatous sheath in the outer cortex of the rhizome.

B. Leaf

Petiole (Fig. 13·12). A transverse section of the petiole is almost circular with distinct adaxial groove. Next to the single

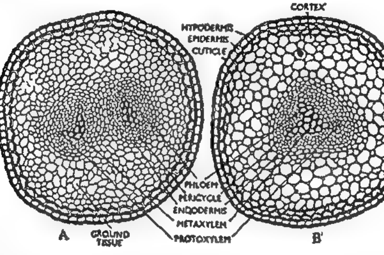

Fig. 13·12. *Adiantum capillus-veneris* L. (A—B). A. T.S. through the base of the petiole showing two meristeles. B. T.S. through the petiole a little above the base showing a single meristle which is three angled. The two meristeles have fused together to form one trace.

layered epidermis is one to many layered hypodermis (*Fig.* 13·12) next to which lies the ground tissue. Number of vascular strands entering the petiole depends upon the number of traces given off by the stele to each leaf (Nayar, 1962). In *A. caudatum*, *A. edgeworthii* and *A. philippense* only a single gutter-shapped vascular strand enters the petiole. In *A. capillus-veneris* and many other species two band-shaped vascular strands enter the petiole (Fig. 13·12, A). During their course upwards they unite and form one bundle (Fig. 13·12, B). The xylem bands of the vascular bundles are often slightly curved with the concavity facing outwards and is thickest in the middle, becoming gradually thin towards either margin where the protoxylem is located (**exarch**). In *A. bausei* a small patch of included parenchyma is present in the xylem band. The ends of the xylem band may become hooked in some species (*A. peruvianum*, *A. tenerum* and *A. polyphyllum*).

Lamina (Fig. 13·13, A—C). The lamina exhibits an internal structure usual for the mesophytic leaves. It has the two epidermal

layers bounding an undifferentiated mesophyll whose cells are armed. The epidermal layers are covered by a thin cuticle. In some species, *e.g.*, *A capillus-veneris*, *A. thalictroides* and *A. pedatum* there is only one or two layered mesophyll (Fig. 13·13). In *A. pedatum* the mesophyll is entirely lacking in some regions of the lamina and at such places the two epidermal layers are contiguous. Both the upper and the lower epidermis are usually chlorophyllous. The epidermal cells over the veins are non-chlorophyllous, highly elongated and narrow with tapering ends. The walls of these cells are hyaline and pronouncedly thickened. In *A. macrophyllum* groups of thick-walled cells occur scattered throughout the upper epidermis. The stomata are irregularly distributed throughout the surface of the leaf.

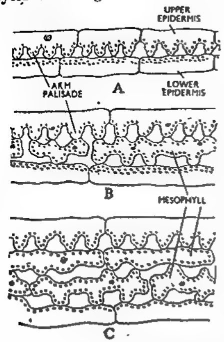

Fig. 13·13 (B—C). Sections through two types of leaves of *Adiantum capillus-veneris* showing variations in the internal structure.
A. Section through leaflet of *A. pedatum* showing complete absence of mesophyll.

In *A. flabellulatum* the stomata are aggregated to areas near the veins. Both uniseriate and multiseriate hair have been recorded on the epidermis. In *A. caudatum* and *A. hispidulum* the epidermis bears small palae or ramenta. In species with thin lamina the veins are not surrounded by any bundle sheath (*A. pedatum*). In species with thick lamina the veins are surrounded by a sheath of sclerenchyma which extends towards either epidermis to merge with the specialised epidermal cells over the veins (Nayar, 1962), *e.g.*, *A. macrophyllum*. The phloem in the vascular bundle of the vein lies towards the lower epidermis and xylem towards the upper epidermis.

Root. The root is diarch like that of *Dryopteris* and *Pteris*. The cortex may be wholly sclerenchymatous or partly so. The endodermis is very distinct and has casparian bands. The epidermis when intact is made up of smaller cells with their walls coloured brown. For figure refer to that of *Dryopteris* (11·6).

SPORE PRODUCING MEMBERS

Sporophylls. There is no difference in the structure, form and shape of the sterile and fertile leaves. Any leaf is capable of bearing sporangia. The whole leaf may bear sporangia or a part of it may become sporangiferous. The sori are borne at the distal ends of the pinnae or pinnules (Fig. 13·14) and consist of sporangia superficially over a short portion towards the distal regions

of the veins. The ultimate ends of the veins do not bear sporangia so that the sori are not marginal in position. They are submar-

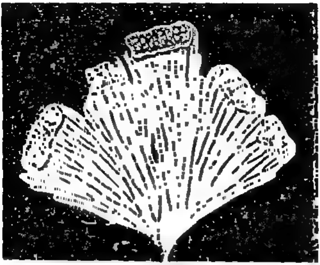

Fig. 13·14. A sporophyll of *Adiantum capillus-veneris* as seen from ventral side.

ginal. The complete sporangia bearing region of the leaflet or the pinnule folds downwards and usually loses chlorophyll during the course of its development. It forms the **false indusium.** The sporangia usually develop on the infolded portion of the pinnule but may in some cases spread slightly on the surface covered by the folding (Nayar, 1962). The sporangia may develop at the distal ends of all the veins of a pinnule (*A philippense*) and form a continuous sorous or the sporangia develop only at the distal ends of some veins in which case small and separate sori are formed. In the sori of *A. tenerum*, *A. bausei* and *A. rubellum* the sporangia are interspersed with small paraphyses (Nayar, 1962). The paraphyses are small uniseriate hair like structures with a one or two celled stalks bearing a globular terminal cell with dense hyaline contents.

Sporangia (Fig. 13·15). The sporangium has two well defined regions: (*i*) the stalk and (*ii*) the **head** or the **capsule**, The stalk

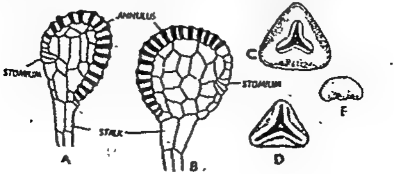

Fig. 13·15. Sporangia and spores of *Adiantum*. (After Nayar)

is made up of three rows of cells, each row about 4 cells long (Nayar, 1962). The sporangial stalk is primarily made up of two rows of cells, the third row is formed secondarily during sporangial development from one of the basal cells of the sporangial head. The head or the capsule is shaped like a biconvex lens (Fig. 13·15). It has a single layered wall enclosing the spores. The wall has a distinct vertical **annulus** of 12-24 cells long. The annulus is separated from the stalk by one or two ordinary thin walled cells. The **stomium** is also not continuous with the annulus and the stalk. From the annulus it is separated by two (*A. capillus-veneris*) to six (*A. thalictroides*) wall cells, whereas from the stalk it is separatde by two or three wall cells. The rest of the sporangial wall is composed of a few large cells that have a regular outline. The sporangial stalk lacks water gland.

The development of the sporangium is exactly similar to that of *Dryopteris*.

GAMETOPHYTE

Spores (Fig. 13·16). The spores are the pioneer structures of the gametophyte generation. The spores in *Adiantum* are tetrahedral (Fig. 13·17) and have a triangular amb with concave sides.

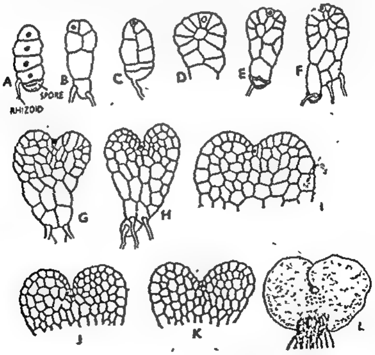

Fig. 13·16. *Adiantum*, germination of spore and formation of mature prothallus. (After Nayar)

The uninucleate spore protoplast is surrounded by a two-layered wall. The outer wall or the exine is smooth and yellowish brown

or deep brown. In *A. caudatum*, *A. tenerum*. *A. peruvianum* and *A. trapeziforme* the exine is marked with faint granulations. The triradiate ridge or the **laesura** is short and has thin margins. In *A. venustum* it has slightly thick margin.

Germination of the spore (Fig. 13·16, A—L). The spores germinate on falling on a suitable substratum. The exine ruptures at the triradiate ridge and the intine protrudes out in the form of a germ tube. It encloses the protoplasts. A lateral rhizoid arises from the germ tube The germ tube becomes a filament of 4—6 cells long (Fig. 13·16, A). The cells develop chloroplasts and become green. The cells are barrel shaped. The terminal cell of the filament divides by two oblique walls to cut off a three-sided meristematic (apical) cell. The lower cells of the germ filament may divide longitudinally, either all of them (*A. bausei*, *A. tenerum* and *farleyeriae*), or only a few upper ones lying below the
The apical meristematic cell divides along the three faces

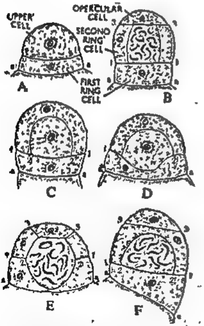

Fig. 13·17. Stages in the development of antheridium in *Adiantum lunulatum*. (After Verma and Khullar)

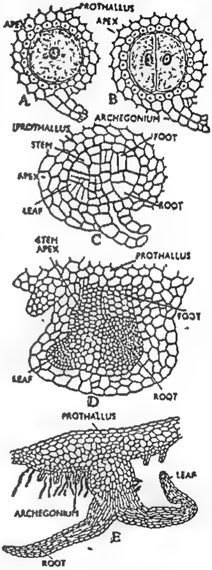

Fig. 13·18 (A—E). Various stages in the development of embryo in *Adiantum concinnum* (A—C) and *A. capillus-veneris* (D—E).

to the formation of a spathulate plate of cells (Fig. 13·17, E, F). During further division the apical cell becomes narrow or almost spindle shaped (Fig. 13.16, E, F). It persists till the prothallus assumes its characteristic cordate form (Fig. 13·16, G—H). Later it is replaced by an apical meristem of two cells lying in a deep apical notch (Fig. 13·16, J, K). The cells dehind the apical notch divide in horizontal plane to form a thick cushion. The wings of the prothallus are only one layer of cells in thickess and are usually parenchymatous In some species (Nayar, 1962) collenchymatous cells have been noticed at the corners.

The structure and development of an antheridium (Fig. 13·17) and archegonium (Fig. 11·23) is similar to *Dryopteris*. The development of embryo also follows the same course as of *Dryopteris*. There are minor differences as illustrated in fig. 13·18; A—E.

YOUNG SPOROPHYTE

Generally a prothallus bears only one sporophyte but under experimental conditions 2 or 3 sporophytes per prothallus have also

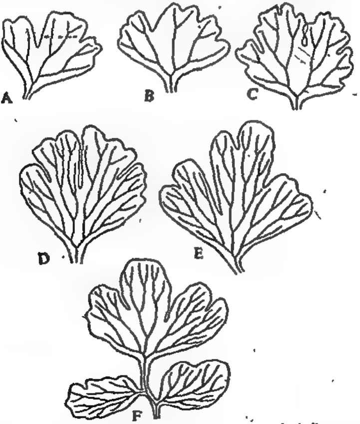

Fig. 13·19. Adiantum capillus-veneris. The juvenile leaves (A—F). (After Nayar)

been noted (Nayar, 1962). Apogamous development of the sporophyte from the median and cushioned region has been reported in

A. philippense (Mehra, 1928, 1949). During normal embryonal development the first organs to make their appearance are the root and the juvenile leaves. The stem develops late. The primary root penetrates the soil and establishes itself. The juvenile leaves are usually divided (simple in *A. flabellulatum*) as in *A. capillus-veneris* (Fig. 13·19) and all other species. In this case the lamina of the juvenile leaf is two lobed, and is traversed by a dichotomously branched mid rib (Fig. 13·19, A, B). Later the lamina expands and becomes three lobed (Fig. 13·19, C). The tip of the lamina elongates and a number of lateral lobes appears (Fig. 13·19, D—E) and the leaf becomes pinnate (Fig. 13·19). The mid-rib in all cases loses its identity towards the apex, dichotomising many times like other veins, but towards the base it maintains its identity and bears lateral veins in alternate succession, each lateral vein entering a separate lobe of the lamina and dichotomising four to five times. In tripinnate leaves (*A. capillus-veneris*, *A. venustum*) the lateral lobes themselves establish mid-rib (Fig. 13·20), which is less prominent than main mid-rib.

CHAPTER XIV

PTEROPHYTA—LEPTOSPORANGIOPSIDA—MARSILEALES

The order Marsileales of the class Leptosporangiopsida includes a small group of aquatic or semi-aquatic ferns. They are all included in a single family Marsileaceae. The chief order and family characters are :

(*i*) They are all heterosporous ferns.

(*ii*) The sporangia are produced within a special structure called the sporocarp.

(*iii*) The sporangia in the sporocarp are arranged in small groups called the sori. The sori are gradate.

(*iv*) Each sorus is bisporangiate and contains both mega and microsporangia.

(*v*) The number of sori per sporocarp varies from two to many.

(*vi*) Circinate ptyxis of the leaf in the bud condition.

(*vii*) Laminar nature of the sporocarp.

The family marsileaceae is represented by 3 living genera, [illegible] — and *Marsilea*. All the three are [illegible] *Pilularia* has 6 species. *Regnelli*- [illegible] characteristic in being the only [illegible] produces latex (Labourian, 1952). *Marsilea* is represented by 53 living and 10 fossil species. It is usually considered as a type.

MARSILEA L.

Distribution. This best known genus of the family Marsileaceae is world-wide in distribution. *However it is rich in species* in the warmer parts of the world such as tropical Africa and Australia. *It is well represented in the northern hemisphere.* About *9 living species have been recorded from* India. Of these *Marsilea minuta* is the commonest. [illegible] In the Punjab it is very comm[illegible] *M. quadrifolia*, *M. rajasthanensis* [illegible] important Indian species.

Habitat. Some species suc[illegible] and [illegible] are hydrophytic. They grow sub[illegible]

The sporocarps are produced under water. Some species are amphibious. They grow after the rains in temporary shallow ponds and puddles (*M. aegyptiaca*). They fruit only under dry, terrestrial conditions when water dries up. Examples are *M. vestita* and *M. aegyptiaca*. A few species of *Marsilea* are **xerophytic.** They grow on dry land (*M. condensata, M. rajasthanensis*). The tropical example of this category is *M. hirsuta*. All the species are rooted either in the mud or soil.

SPOROPHYTE

External Morphology. The *M*... leaved ... es (Fig ... with ... multicellular and unbranched.

Stem. The stem is long and slender (Figs. 14.1, 14.3). It creeps either on the surface like a **stolon** or slightly below the ... rhizome. It has an indefinite power of growth ... arise at the bases of leaves. According to Hanstein they are axillary in position. Puri and Garg and Sachs consider them lateral to the leaves as a rule. Bower also considers the branches to be extra-axillary in position arising in the

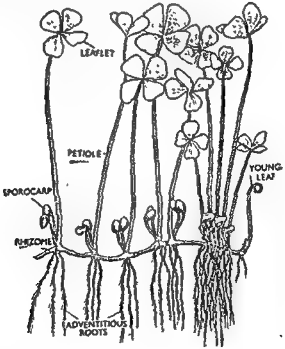

Fig. 14·1. Portion of sporophyte of *Marsilea minuta* showing habit.

lateral or oblique position, indicating the dichotomy of the axis. They run in all directions and may get rooted at the nodes. In this way a single plant may cover an extensive area about 20 metres in

diameter or even more. The stem is divisible into distinct nodes and internodes. The internodes are long in the hydrophytic plants and short in the sub-terrestrial or xerophytic species.

Roots. The primary root is short-lived. All others are adventitious and arise gradually at the nodes (Figs. 14·1 and 14·4) on the underside of the stem. Occasionally they may arise from the internodal region. They are thin and may be branched or unbranched. Their number at each node may be one or more. The branching is monopodial. The branch roots are arranged in two rows and are developed in an acropetalous succession.

Leaves. The leaves arise from the upper side of the stem alternatively and are arranged in two rows (Figs. 14·1, 14·3). They are petiolate and compound. The petioles of the submerged plants are long, thin and flexible with the lamina floating on the surface of water. The leaves of plants growing on mud or land have upright, short petioles with the lamina held in a spreading position. The compound lamina is divided into four leaflets of the same size. They spring from the tip of the petiole so that the leaf apparently looks **quadrifoliate.** Actually it is **quadrijugate** as the four leaflets are arranged in a pinnate manner. *Two of* them form the distal pair and the other two form the proximal pair (Fig. 14·5, F). The leaflets of the proximal pair are really alternate. Occasionally the number of leaflets may be 5 or 6 or even 8 instead of the usual number 4. In outline the leaflets are obovate to obcuneate or wedge-shaped. The margin is variable. In many species it is entire. In *M. minuta* and other hydrophytic species the outer margin of the leaflet varies from entire to crenate or toothed, whereas in the terrestrial species (*M. aegyptiaca* and *M. rajasthanensis*) it varies from crenate to slightly deeply lobed (Gupta). The venation is [illegible]. It is a closed reticulum. The veins of [illegible] manner. The branch [illegible] also united near the margin by *loop veins* (*Fig. 14·5*). The leaflets exhibit sleeping movements. At night the pinnae become folded upwards. The young leaves have circinate ptyxis in the bud.

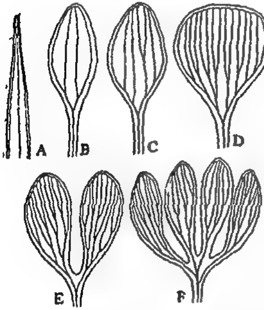

Fig. 14·5. **Marsilea.** Ontogeny of the pinnae. The venation is dichotomous. The vein endings form loops so that ultimate vein ends are fused. (After Braun)

Asexual reproductive bodies

Sporocarps. When water begins to dry up the leafy plant bears special, u ... bodies called the **sporocarp** ... bisporangiate. The stalk may ... **peduncle** or **pedicel.** The shape, size and contents of the sporocarp, and the attachment of its pedical to the petiole of the leaf vary considerably. For details on these points refer to asexual reproduction.

Tubers. The stem towards the end of the growing season in some species (*M. hirsuta, M. minuta*) bears resting propagation bodies called the tubers. The tubers function as perennating structures sprouting on the advent of the season favourable for growth.

ANATOMY

(a) Stem. (*Fig.* 14·6). Viewed in a transverse section the mature stem or rhizome is circular in outline. It has a concentric arrangement of the permanent tissues. The tissues composing it are arranged in three zones, **epidermis, cortex** and the **stele.**

... ms the outermost protective portion ... cells. The epidermal cells are thick- ... without any stomata. It is perma- ...

2. **Cortex.** It lies internal to the epidermis and is several layers thick. It is differentiated into three regions, the **outer cortex,** the **middle cortex** and the **inner cortex.** The outer cortex is parenchymatous and may be one to several cells in thickness. The parenchyma cells are compactly arranged. Here and there among them occur a few tannin cells. The ring like outer cortex of compactly arranged parenchyma cell serves to maintain the cylindrical form of the stem. The **middle cortex** which lies internal to the outer cortex consists mainly of air cavities. The aerenchyma is an air storage tissue consisting of a single layer of air chambers arranged in a ring. The chambers are separated from one another by single layered partitions consisting of thin walled parenchymatous cells. The **inner cortex** is a solid tissue of several cells in thickness. The outer cell layers of the inner cortex are thick-walled or sclerotic constituting the sclerenchyma. The inner layers of cells are compactly arranged and parenchymatous. Some of these cells may contain tannin, others are filled with starch. In the xerophytic species (*M. aegyptiaca*) the air chambers in the middle cortex become obliterated.

3. **Stele.** The vascular cylinder is medullated. The **xylem** ...

... is **outer endodermis, outer pericycle, outer phloem,**

inner phloem, inner pericycle and **inner endodermis.** The medulla or pith, which is delimited by inner endodermis, occupies the centre. Its structure like that of the middle cortex depends upon the habitat in which the plants grow. It is parenchymatous in the plants growing in water. It becomes more or less sclerotic in plants growing in mud or damp soil (Fig. 14·6). In the xerophytic

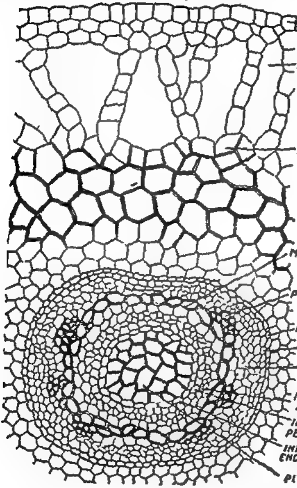

Fig. 14.6. T.S. through older portion of the rhizome of *M. minuta* showing sclerenchymatous pith.

species it is sclerenchymatous. *M. vestita* has exarch xylem with well defined protoxylem elements. *M. aegyptiaca* has mesarch protoxylem (Gupta and Bhardwaja). In *M. quadrifolia* and others protoxylem elements are not conspicuous. In a section passing through or near the node, the vascular cylinder consists of two parts, an arc-like or C-shaped stele and a small curved vascular strand. The latter represents a **leaf trace.** The inner and outer layers of endodermis, pericycle and phloem become continuous at the ends of the arc-like stele. This is an **amphiphloic solenostele.** Vessels have also been reported in some specis of *Marselia.*

(*b*) **Petiole** (Fig. 14.7). The internal structure of the petiole is similar to that of the stem. There is the single layered **epidermis**

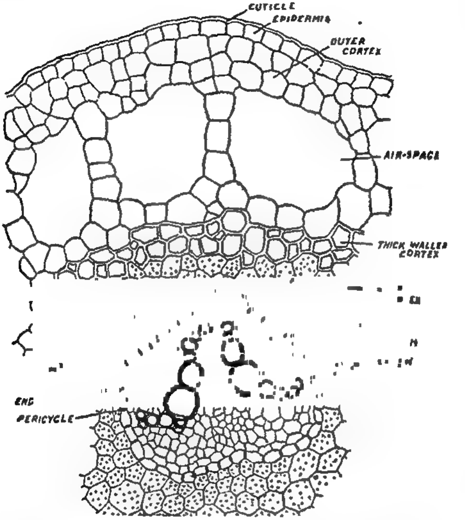

Fig. 14·7. T.S. petiole of *M. minuta*.

made up of rectangular cells. Beneath it are a few layers of thin walled cells that constitute the **outer cortex.** This is followed by the aerenchymatous **middle cortex** which consists of a ring of air chambers. The air chambers, as in the stem, are separated by single layered partitions of thin walled parenchyma cell. The air spaces tend to disappear in drier habitats. The inner cortex is a solid, compact tissue several cells deep. The outer cell layers are sclerenchymatous (Fig. 14.7). The inner layers of cells are parenchymatous and are filled with starch. Here and there tannin filled cells also occur. The inner cortex is delimited by a single layered **endodermis.** Within the endodermis is the stele which is somewhat triangular in outline. It lies in the centre and has a single **vascular bundle.** The xylem part of the bundle

[illegible] arm has one [illegible] smaller ones [illegible] is the xylem parenchyma. Surrounding the xylem is the **pholem** followed by the **pericycle.** The pericycle is bounded by the endodermis.

(c) **Leaflet** (Fig. 14·8) The leaflet in a transverse section reveals the following structure:—

(i) **Epidermis.** Is forms the boundary. There is thus the **upper epidermis** and **lower epidermis.** Both are single layered and have slightly sunken **stomata.** In the hydrophytic species with floating leaves they are restricted to the upper epidermis only. As the water dries up and the leaflets become aerial the stomata develop in the lower epidermis as well. According to Gupta the stomata are fewer but bigger and the epidermal cells have more wavy walls in plants growing under drier habitats than those found in water.

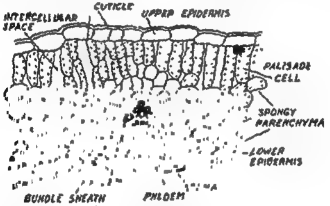

Fig. 14·8 V.S. pinna or leaflet of *M. minuta.*

(ii) **Mesophyll.** The tissue that lies between the upper and lower epidermis is called the **mesophyll.** It is differentiated into palisade and spongy parenchyma. The former lies beneath the upper epidermis and consists of columnar cells rich in chloroplasts. The spongy parenchyma which faces the lower epidermis consists of rounded cells. Just beneath the lower epidermis are the large *air* chambers. They are separated by septa. Submerged leaves, however, show no distinction into the palisade and spongy tissues.

(iii) **Vascular bundle.** Embedded in the mesophyll tissue are vascular bundles. They are concentric in nature. Each bundle has a central core of xylem surrounded by phloem. Externally bundle is bounded by the single layered endodermis. *It is distinct.*

(d) **Root** *(Fig. 14·9). In a transverse section* it consists of the piliferous layer, cortex and stele.

(i) **Piliferous layer.** It is the surface layer consisting of compactly arranged biconvex cells. The outer walls of the cells are thickened.

(*ii*) **Cortex.** It lies within the piliferous layer and is several layers thick. It shows distinction into **outer cortex** and **inner**

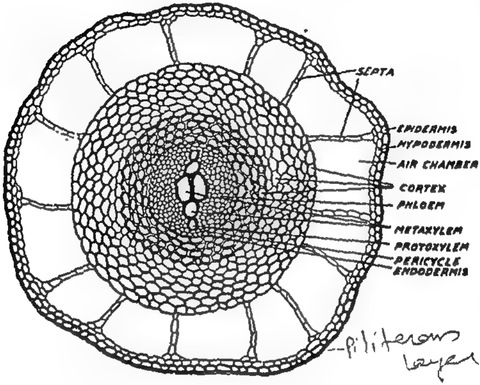

Fig. 14·9 A. T.S. root of *M. minuta.*

cortex. The outer cortex is **aerenchymatous.** The large air chambers are arranged in the form of a ring and are separated from each other by longitudinal septa. The inner cortex is compact. It consists of rounded cells containing starch. They often become sclerenchymatous under terrestrial conditions.

(*iii*) **Endodermis.** The inner cortex is delimited by the endodermis. It is distinct and consists of a single layer of cells.

(*iv*) **Stele.** It lies within the endodermis and is usually **diarch** and **exarch** rarely **monarch.** It consists of the pericycle and the vascular tissues. There is no pith The pericycle consists of a single layer of cells just within the endodermis. Within the pericycle is

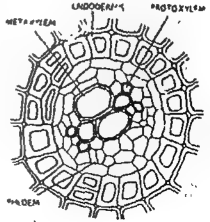

Fig. 14·9 B. Portion of stele of root of *Marsilea minuta* showing diarch xylem.

the vascular tissue consisting of xylem and phloem. The xylem which is plate-like occupies the centre of the stele. In the middle of the elongated xylem plate are two large and two small metaxylem elements. The protoxylem is **exarch.** It consists of two small masses of still smaller protoxylem cells one at each end touching the pericycle. On either side of the xylem plate is the band like phloem. There are thus two xylem bundudles and two phloem. They are situated on alternate radii. Recently White reported the occurrence of vessels in the roots of certain species of *Marsilea.*

REPRODUCTION. *Marsilea* reproduces vegetatively as well as by means of spores that are of two types (heterosporous) and on germination give rise to two types of gametophytes.

Perennating str

Vegetative Reproduction

Vegetatively *Marsilea* plants reproduce by the formation of tubers. They are small, bud like structures. Morphologically they are the modified side branches. Each tuber contains reserve food material in the central portion and is covered with minute reduced scale leaves. It serves as a perennating organ, sprouting with the return of conditions favourable for growth. Tuber formation has been reported in *M. minuta* and *M. hirsuta*

SPORE FORMATION

Marsilea is heterosporous. The micro- and mega-sporangia are borne in special bean-shaped bodies called the sporocarps. The former produce many microspores (32-64) whereas the megasporangia contain only one megaspore.

Sporocarp. A. Morphology. The sporocarps are bisporangiate and are borne on short or long stalks called the **peduncles** or **pedicels.** They appear on the plant when it has reached a certain stage of maturity. In some species they appear when the water in the ponds begins to evaporate rapidly and its level falls considerably, but are always produced under water. In others they are produced when water completely dries up and the plants become terrestrial. The pedicel or peduncle of the sporocarp is attached to the petiole. The petiole and the grouping of the sporocarps varies considerably. Gupta puts the various species of *Marsilea* under three well defined categories according to the mode of attachment of pedicel with the petiole:—

(*i*) Pedicels directly inserted on the petiole in a linear sequence on the same side (Fig. 14·10, A). Examples are *M. polycarpa* and *M. subangulata.* Both are foreign species. No Indian species belong to this category. In *M. coromandelica* (Fig. 14·10, D) and *M. vestita* the peduncle of the solitary sporocarp is directly attached to the base of the petiole.

(*ii*) Pedicels united with one another and then jointly inserted on the petiole. The common Indian example is *M. quadrifolia* (Fig. 14·10, B).

(*iii*) Pedicels free or slightly connate and attached to the base of the petiole. The common Indian species, *M. minuta*, is the best example of this type of attachment (Fig. 14·10, C).

Many variations from the above-mentioned three types have been recorded in nature. Conditions intermediate between the first and second types were recorded in *M. quadrifolia* (Gupta, 1961). When young, the sporocarps are soft, green and covered with hairs. At maturity they become brown to dark brown, hard and nut like. The hairs persist in the terrestrial species but disappear at maturity in the aquatic species. In shape the sporocarps are oval or bean shaped in *M. minuta* and other hydrophytic species, but squarish or rectangular in *M. aegyptiaca*, *M. rajasthanensis* or other xerophytic species (Gupta, 1961). Just beyond the point of attachment of the

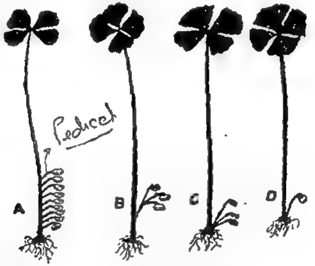

Fig. 14·10. Mode of attachment of the sporocarps to the petiole.
A. *Marsilea polycarpa*
B. *M. quadrifolia*
C. *M. minuta*
D. *M. coromandelica.*

sporocarp to the stalk (raphe) are often present one or two teeth like protuberances, at the back in the median plane. They are known as the **horns or teeth.** In *M. minuta* both the teeth are prominent. *M. quadrifolia* has the lower tooth conspicuous and the upper blunt. In *M. aegyptiaca* the upper tooth is blunt and prominent. The lower is absent. In *M. uncinata* the teeth are spine-like projections, with the upper one more conspicuous than the lower. There are some species in which teeth on the sporocarp are lacking.

B. Internal Structure (Figs. 14·11, 14·12, 14·13).

(*i*) **Wall of the Sporocarp** (Fig. 14·11). The bivalved sporocarp has a thick and resistant wall. A mature sporocarp has a three layered wall. The outermost layer is made up of broad and

columnar cells. It is called the **epidermis** and its continuity is interrupted by stomata. It is covered with cuticle and bears hair in young sporocarps. Next to the epidermis is the two layered **hypodermis**. These two layers are often designated as the outer and inner **palisade layers**, respectively. The cells of the outer layer are elongated and thick walled whereas those of the inner layer are more elongated and have thin walls. Their contents are vacuolated. Both the layers have chloroplasts in their cells. Next to the hypodermal layers is a layer of **hourglass like cells** whose walls are also thick. Inner to this layer is a parenchymatous tissue of variable thickness. These cells gelatinise in a mature sporocarp and help in its dehiscence. They form a gelatinous tissue called the **sporophore** that runs around the sporocarp cavity, in a dorsiventral plane.

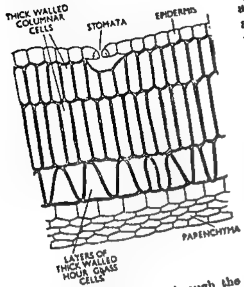

Fig. 14·11. T.S. through the wall of sporocarp of *Marsilea minuta*.

(*ii*) **The Sori.** The sori are elongated and arranged in two alternating rows in the cavity of the sporocarp, each row lies in the cavity of the valve and is situated dorsiventrally and transversally to the long axis of the sporocarp. Each sorus arises on a ridge-like placenta or the receptacle that is borne on the sporocarp wall (Fig. 14·12, A) and is covered by membranous indusium made up of two layers of cells. The sori overlap each other and the indusia of adjacent sori are partially fused. The number of sori in a sporocarp varies form two (*M. aegyptiaca*) to twenty (*M. quadrifolia*, *M. vestita*). There are 11-12 sori in *M. minuta*. Each sorus bears both **megaand microsporangia**. The former are short-stalked, and are arranged in a row at the tip of the receptacle, whereas the latter are long stalked and arise on the sides. Their number in a sorus varies with species. In *M. minuta* a sorus has 4—8 megasporangia and 8—13 microsporangia. In *M. aegyptiaca* there are 5—16 mega- and 9—19 micro-sporangia. Megasporangia are sometimes absent in sori of *M. minuta*, *M. rajasthanensis* and *M. vestita*.

Mehra and Loyal (1960) reported three biotypes of *M. minuta* :—(*i*) A biotype with normal micro and megasporangia. The megasporangia have one megaspore. (*ii*) Sporocarps with abnormal microsporangia that have different shapes and sizes of microspores and normal megasporangia with one megaspore. (*iii*) A biotype with abnormal mega- and microsporangia. The former have many sterile megaspores, the latter have also many microspores of different shapes and sizes. They recorded $n=20$ in *M. minuta*.

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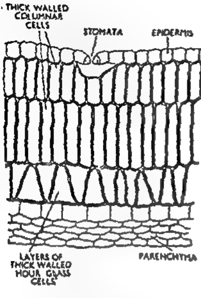

Fig. 14·11. T.S. through the wall of sporocarp of *Marsilea minuta*.

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In a horizontal section the sori are seen to be arranged in two alternating rows (Fig. 14·12, A). This section reveals the exact num-

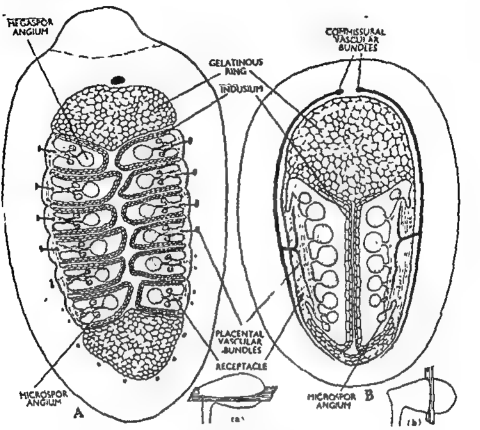

Fig. 14·12 (A—B). Internal structure of sporocarp. A. Horizontal section through sporocarp. B. Vertical transverse section through sporocarp (*a* and *b* indicate planes of sections).

ber of sori in the sporocarp. The megasporangia are seen at the apex of the receptacle and develop first whereas microsporangia are on the sides and develop later. The sorus is thus gradate and sporangia develop in a basipetalous manner. The placental vascular bundles and commissural bundle are cut in a transverse plane. The gelatinous ring appears in the form of two big masses at either end. The pedicel is also cut transversely.

A [illegible] The sori [illegible] sporangi[illegible] side of t[illegible] is clear. The stalk is not cut in this section. The commissural bundles, the placental bundles and placental branch are very clear. The sporophore appears as two distinct masses on the dorsal and ventral sides.

In a vertical longitudinal section (Fig. 14·13) or sagittal section the pedicel is also cut longitudinally and the gelatinous ring is seen

to surround the sori, which are seen to contain either mega- or microsporangia depending upon whether the section passes through

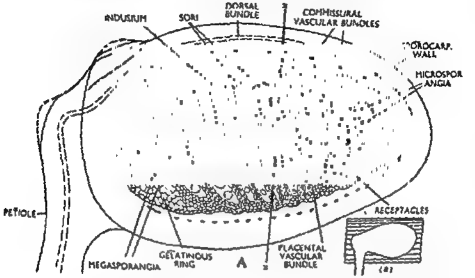

Fig. 14·13. A vertical longitudinal section through the sporocarps.

the former or the latter. The dorsal vascular bundle is seen in continnation with vascular strand of the pedicel. The commissurals are cut transversely and can be seen around the gelatinous ring. A section passing through the microsporangia shows the placental bundles also.

Vascular Supply of *Sporocarp* (*Fig.* 14·14). The vascular bundle of the pedicel of the sporocarp runs upwards and without

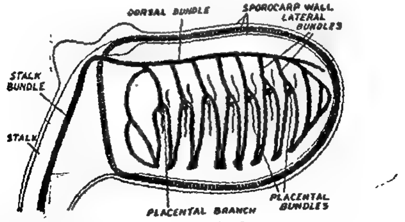

Fig. 14·14. Showing vascular supply of the sporocarp.

undergoing any change reaches the point of attachment of the body of sporocarp and the pedice
tooth of the sporocarp (Fig.
upper or the dorsal side of t...

The dorsal bundle gives off **lateral** all along its length. The number the number of sori. These lateral the sori situated in either valve of the sporocarp. After giving off the last pair of lateral bundles the dorsal bundle bifurcates into two branches that supply right and the left valves of the sporocarp (*M. minuta*. Puri and Garg, 1953). The wards the ventral This bifurcation is downwards. The adjacent branches of the bifurcated laterals anastomose near the etwork (Fig. 14·14).

placental bundles are not given off from the first and the last pairs of lateral bundles, because there are no receptacular ridges in this area.

1898) gave a *trifolia*. The af (Fig. 14·15, appears after he young leaf sporocarp initial differentiates (Fig. 14.15, A). This cell behaves just like the two sided leaf apical cell and cuts off segments on either side. One of these segments may behave as apical cell of the second sporocarp and so on for the third sporocarp. This means that the two or the three sporocarps are ontogenetically the primary, secondary and tertiary branches of the leaf.

de and forms a that its distal es further and egments cut off pidermal layer re thin walled leaf segment. of the young marginal cells appear on the (ventral) and **soral canals**. Each the indusium. This soral mother cells anged in two alter- sium (Fig. 14·15, E). ring further growth lders of the sporo- sporangial initials he soral canals (Fig. the receptacle and The other initials appear along the sides and grow into microsporangia. The megasporangia thus develop first and are older than the microsporangia.

Morphological Nature of the Sporocarp. Two main interpretations have been put forth to explain the morphology of the sporocarp of *Marsilea*. These are :—

(a) **The Laminar or Leaf Segment Hypothesis.** This hypothesis believes that the sporocarp is a modified lateral, fertile

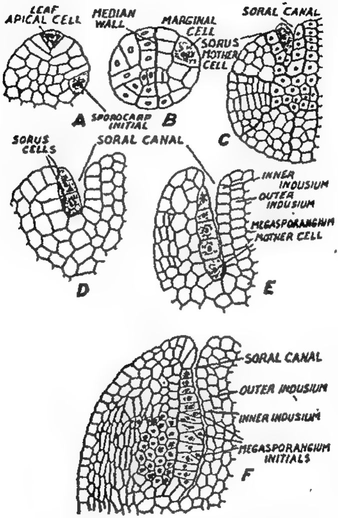

Fig 14·15. Stages in the development of sporocarp in *M. quadrifolia.* (After Johnson)

segment of the leaf or frond. It has been supported by majority of the workers whose views are given below :—

Russow (1872) and Busgen (1890) regarded the sporocarp of *Marsilea* to be composed of two leaflets whose ventral surfaces face each other.

Goebel (1882, 1905, 1930) considered the sporocarp to be a fertile leaflet, or the pinna. He considered that the sporocarp without its sporangia is comparable to a single leaflet of the sterile leaf of *Marsilea*.

Eames (1936) compared the sporocarp to the tip of the leaf with

four leaflets. He postulated that the body of the capsule represents the two distal leaflets whereas the hump of the sporocarp with two teeth represent the remains of the proximal leaflets (Fig. 14·17, A, B). He considered the hump as reduced proximal pair

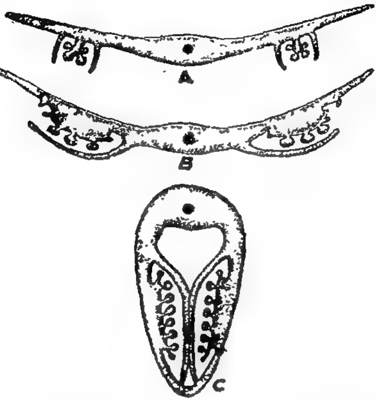

Fig. 14·16 (A—C). Smith's view of the morphological nature of sporocarp. (After Smith)

of leaflets. His conclusions are based upon the similarity of course of vascular bundles in the sporocarp and the four leaflets of a sterile leaf. In *M. quadrifolia* the main vascular bundle sends two vestigeal branches into the lower tooth. This suggests that the hump represents the remains of the proximal pair of leaflets.

Smith (1938, 1955) compares the sporocarp of *Marsilea* to an enfolded leaflet (Fig. 14·1 [illegible] by a single midrib (Fig. 14·16, [illegible] ateral veins on either side. He [illegible] the enfolded leaflet of a lept [illegible] a-hea-ceae) bearing gradate sori on its abaxial side (Fig. 14·16, B—C). The gradate sori in *Marsilea* and presence of distinct indusia support Smith's viewpoint that the sporocarp of *Marsilea* is comparable to the enfolded pinna of a Cyatheaceous fern (Fig. 14·16, A—C).

Takhtajan (1953) stated, "the sporocarp of the Marsileales may

be considered a more specialised fertile segment of a leaf of the type common to Schizeaceae."

Puri and Garg (1953) have discussed in detail the literature regarding the morphological nature of the sporocarp (Fig. 14·17, C). While commenting upon its

state, to a of as or of ateral

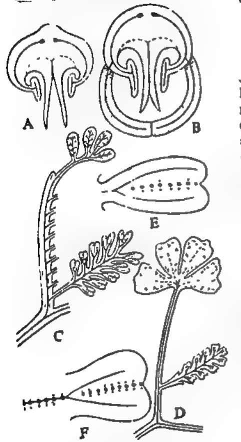

Fig. 14·17. Morphological naetur of sporocarp. A—B. Eames view of morphlogical nature. C. Representing Puri and Garg's view D—F Representing Gupta's viewpoint.

bundle midrib observ sporoc end of of the supply is leaflets and hence the laminar nature of the sporocarp is fully supported.

Gupta (1962) also supported the laminar nature (Fig. 14·17, E—G) of the sporocarp. He regards the sporocarp to be a leaflet with as many marginal lobes as the lateral bundles. He does not regard the sporocarp to be a compound structure formed by the concrescence of the pinnules. In his opinion the pinna or the leaflet was only lobed and not divided into pinnules as is regarded by Puri In his own words, "to

situated on their sides. sions of these lobes (Fig. 14·17, E) rather than on their sides. Consequently they get their vascular supply from the midrib bundles, that is at the point of bifurcation of the commissurals themselves."

of opinion favours the laminar nature of the an interpretation can be laminar or leaf segment

theory) :—

1. The sporocarp develops from a marginal cell of the leaf. The early segmentation of the sporocarp initial and the leaf initial is similar. Both have two-sided apical cells.

the third sporocarps arise
ie second sporocarp. This
e primary, secondary and

similar to that of
10—15 sporocarps
s manner. All are
borne in a single series on one side of the petiole. The vascular supply to each sporocarp departs from the margin of the vascular bundle of the petiole. Same is the case with the sterile leaflets. The similarity of the vascular supply is clearly indicative of the laminar nature of the sporocarp. Eames (1936) pointed out such a similarity in the case of *M. quadrifolia.*

4. Puri and Garg (1953) also pointed towards a similar nature of vascular supply to the sporocarp and sterile leaflets in *M. minuta.* The vascular supply in both the cases diverges from one end of the V-shaped vascular bundle of the petiole.

5. Busgen (1890) reported certain abnormalities in *Marsilea.* He observed that in *M. hirsuta* some plants bear leaves whose pinnae get modified into sporocarp-like structures. In some cases, he found that the proximal pair of leaflets become very small and the distal ones are comparatively large, valvular, thick and brown. Such teratologies in nature also support the view that the sporocarp of *Marsilea* is a modified lamina or leaflet, specialised for the function of producing spores.

like hypodermis and the
aces simulate the internal

is hypothesis
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cells act as
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and the leaf,

nal cell. Hence the two valves into which the capsule splits at

bursting cannot be homologised with the divisions of the lamina, since these are developed from the numerous sections formed on both sides by the continued activity of the marginal cells. For this reason also any seeming similarity in the branching of the vascular bundle systems of the two organs can have no meaning in the direction of homology" After discussing his viewpoint Johnson concluded, "according to our present knowledge we may consider the capsule as the swollen end of a petiole in which the marginal cells are devoted to the formation of the sporangia instead of a lamina."

SPORANGIA

Marsilea is heterosporous. The **megasporangia** or **macrosporangia** produce **megaspores** (one in each megasporangium) and the **microsporangia** produce **microspores** (32—64 per microsporangium). The sporangia develop in a basipetalous manner on

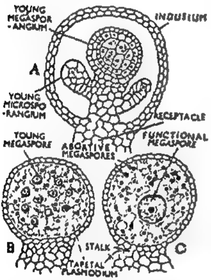


Fig. 14·18 (A—C) *Marsilea quadrifolia*. A. Sorus of *M. quadrifolia* showing indusium, receptacle,

A Megasporangia

(*a*) **Structure.** The megasporangium is an almost spherical structure with a short stalk. It is *larger than the microsporangium* and positioned at the tip of the receptacle (Fig. 14·18, A). It has a single layered jacket of thin walled cells. There *is no annulus*. *Next to the wall are two layers of* ... 14·18, A) that ...gaspore mother ... the tapetal ...8, B, C) and all ...rviving or the functional mother cell undergoes meiosis to form 4 haploid cells out of which 3 degenerate and one grows big to form the megaspore. Kolhatkar (1938). Eames (1936) and Smith (1938, 1955) observed that all the mother cells divide meiotically to produce up to 32 or even 64 spores. Out of these all, except one, degenerate. The surviving one functions as the megaspore (Fig. 14·18, C). *In abnormal sporocarps more than one megaspores may be formed.* At maturity the normal *megasporangium* has one layered wall and contains one large megaspore that almost fills its cavity (Fig. 14·23, *A—B*).

The megaspore escapes by the disintegration of the megasporangial wall. Superficial cell of the

. The
recep-
29, A)
The
three
al cell
along
of the
sporangium (Fig. 14 19, A). The apical cell now divides by an arched periclinal wall towards its outer face (Fig. 14·19, A) This puts an end to the apical growth of the sporangium. This last periclinal division distinguishes an outer smaller **primary jacket cell** and an inner tetrahedral **archesporial cell** (Fig. 14·19, A).

Fig. 14 19. *Marsilea quadrifolia.* Stages in the development of sporangium.
A. T S. young sorus with one terminal megasporangial mother cell and two microsporangial initials.
B—D. Later stages of development.
E. A young microsporangium with microspore mother cells.
F. A mature microsporangium with microspores arranged in tetrads.
G. A mature microsporangium with microspores.

to form a single layered
periclinal walls to cut off
primary tapetal cells which by further periclinal
two layered **tapetum.** The

central primary
spore mother cells
In all 32 to 64 spc:
and only one functions (Fig. 14·18) as the **megaspore.** It grows bigger in size at the expense of others. According to some authors all but one megaspore mother cell degenerate (Fig. 11·22, E). Boterberg (1956) in some species of *Marsilea* and Machis and Rawtischer—Kunkel (1967) in *M. vestita* report the formation of 16 mother cells which form tetrads. Out of these 15 tetrads abort and three megaspores of the sixteenth tetrad also abort leaving behind only one functional megaspore. It grows in size and fills the megasporangium.

Microsporangia. The
sides of the receptacle and are su
oval capsules The structure is si
except that it has 32—64 microspores. The number of microspores varies from 40—64 in *M. minuta* (Gupta, 1962), from 12 to 32 in *M. rajasthanensis* (Gupta, 1962) and 10—32 in *M. condensata*.

The development of the microsporangia is similar to that of megasporangia except that the microsporangia have larger number of microspores

During sporangial development certain changes take place in the wall of the sporocarp. The cells of the hypodermal layer divide by periclinal divisions into two layers. The cells of the outer layer

Dehiscence of the sporocarp

sporocarp. The spores of *Marsilea* remain viable for 20—30 or even 50 years and therefore a long delay in the opening of the sporocarp

The sporophore
along its dorsal side. One of its ends, usually on the ventral side, breaks and the sporophore starts straightening. It comes out of the sporocarp in a looped condition and ultimately straightens in the

form of a long gelatinous cylinder bearing a number of sori (that varies with species) in two alternating rows (Fig. 14·20, A—C). The sori appear as sac like structures and the contained sporangia can be clearly seen. This whole process of liberation of contents, under artificial conditions takes 1-2 hours or even more.

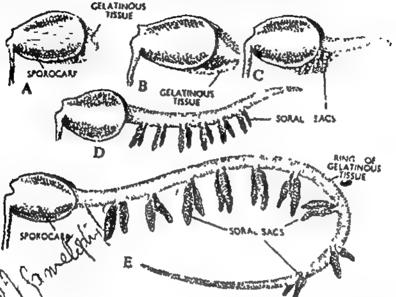


Fig. 14·20 (A—E). Various stages in the dehiscence of sporocarp.

soral sacs gelatinise and al walls also gelatinise and water. This whole process xtrusion of the sporophore. the sporangia and do so

GAMETOPHYTE GENERATION

The microspores and the megaspores germinate separately to produce male (microgametophyte) and the female (megagametophyte) gametophytes. The spores are, therefore, the pioneer structures of the gametophyte or sexual generation.

The microspore is almost yelose in shape, with a faint tri-
:e apex. The microspores vary
re 60 μ in *M. minuta*, 60 to 75 μ
M. aegyptiaca (Gupta, 1962). The
by the inner cellulose cell wall
which in turn is surrounded by
he exine is transparent and may
(1960) studied in detail the
M. hirsuta and *M. diffusa*, res-
ith numerous starch grains. The

Microgametophyte (Germination of Microspore, Fig. 14·21, A—L). The spores absorb water and increase considerably in size. The starch grains move towards the periphery of cytoplasm. The nucleus moves towards the lower side (opposite the pyramidate apex). The nucleus divides into two daughter nuclei, a wall is laid down to distinguish a small lenticular **male prothallus cell** and a large **upper cell** (Fig. 14·21, B, C) or **apical cell**. In *M. vestita* (Campbell, 1892), *M. quadrifolia* (Sharp, 1914), and *M. aegyptiaca* (Gupta 1962) the apical cell divides by a wall diagonal to the first wall into two **antheridial initials** (Fig. 14·21, D, E). In these species there is only one prothallial cell. Belajeff (1898) and Demalsy-Feller (1956) reported that in *M. elata* and *M. diffusa* the upper cell divides to cut off another prothallial cell. Kolhatkar (1937) also described the formation of a second prothallial cell in his *Marsilea* from Poona (*M. poonensis*) There seems to be a variation among the various species of *Marsilea* regarding the number of prothallial cells. Whatever be the case the larger cell or the apical cell after cutting off one or two prothallial cells divides by a diagonal wall into two antheridial initials.

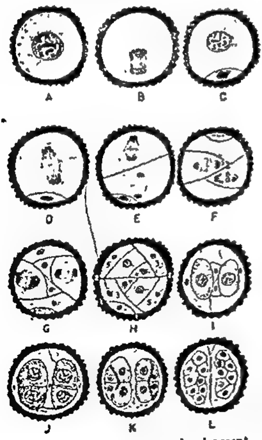


Fig. 14·21. Stages in the development of the male gametophyte in *M. quadrifolia*. (After Sharp)

Each antheridial initial develops into an antheridium containing spermatozoids. Their further development is similar. Each one of them divides by a periclinal wall (Fig 14.21, F) to form an outer wall or **jacket cell** and a wedge shaped sister cell. The latter divides by another periclinal wall laid across its angle into a second smaller jacket cell and a large outer cell (Fig. 14·21, G). The large outer cell divides again by a periclinal wall to cut off an outer or peripheral **third jacket cell** and a central cell or the **primary androgonial cell** (Fig. 14·21, H) So each antheridium has three jacket cells and a primary androgonial cell at this stage. During further development the primary androgonial cell in each antheridium divides simultaneously into 16 **androcytes** (Fig. 14·21, I—L) whose protoplasts metamorphose into multiflagellate spermatozoids.

antheridia disintegrate. The two masses of the androcytes lie free within the spore wall (Fig. 14·21. L). The microspore wall also breaks a little before the maturation of the spermatozoids so that they are liberated in the surrounding water. The whole of this process of development of microgametophyte takes 5—10 hours at 25°—30°C.

Spermatozoids (Fig. 14·22). The exosporium of microspore ruptures at the triradiate ridge. The two androcyte masses are visible through ... nd liberates the contents. ... n mass but sometimes the ... of 4 spermatids (Rice and Laetsch, 1967). Each spermatid cell becomes active and performs slow revolutions which later increase in frequency. The membrane of the spermatids dissolves and releases the spermatozoids. This release is effected by the separation of the spermatozoid from lateral vesicle which remains within the spermatid for about a minute and then disintegrates (Rice and Laetsch, 1967) The whole sequence of release of spermatozoids takes 30 second to one minute in *M. vestita*.

... F, G) has two main ... (*ii*) an anterior nuc-

... kami and Gall (1966) recorded

... tered in it. It varies in diameter from 12—15 μ (*M. vestita*) at the time of release but usually increases to 25—30 μ

... the direction of the anterior coil. The anterior coiled portion of the spermatozoids consists of : (*i*) a continuous band of mitochondrial nature, (*ii*) an elongated nucleus and (*iii*) a series of microtubules that separate the centrioles from the nuclear and mitochondrial portion. The mitochondrial and the nuclear portions are helically coiled. The nuclear helix is be-

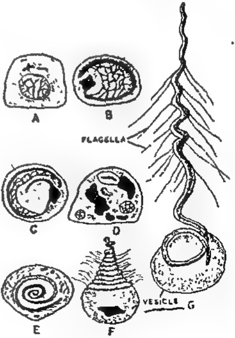


Fig. 14·22 (A—G). Stages in the formation of a spermatozoids (A—E). F—G. Mature spermatozoids. (After Sharp)

hind the mitochondrial helix and is slightly towards its inner side. The mitochondrion and the nucleus are continuous throughout their coiled helix. The mitochondrial part of the helix shows cristae and a certain osmophilic material (Rice and Laetsch, 1967). The flagella are inserted in two rows along the mitochondrial and nuclear portions of the helix. They arise from paired basal granules (centrioles) [illegible] rows. The microtubules are present [illegible] ions and helix (mitochondrial as well as [illegible] in the mitochondrial part of the helix and some from the nuclear part. The flagella are absent in the anteriormost region of the coil.

[illegible] by Rice and Laetsch (1967) in *M. vestita*. In one type the vesicle is very large, whereas in the other type, the posterior vesicle of the sperm bears two anterior coils The latter type of anomaly was also observed by Feller (1957). Rice and Laetsch (1967) record the life span of spermatozoids in *M. vestita* to be 3—3½ hours. They are very active 1—1½ hours after their release.

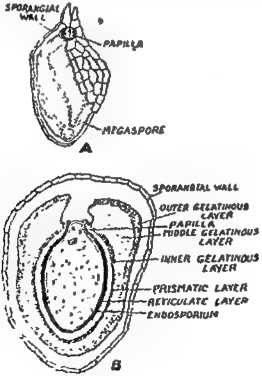


Fig. 14 23 (A—B). Mature megasporangia of *M. diffusa* containing fully mature megaspore. (After Boterberg)

Megaspore. Boterberg (1956) described the structure of the dry megaspore (Fig. 14·21, B) in *M. diffusa*. It agrees in almost all

[illegible]
surrounded [illegible] intine [illegible] endosporium [illegible]
the megaspo[illegible] exine [illegible] exosporium [illegible]
extend over [illegible]

(*i*) The outer gelatinous layer which is of almost equal thickness all round (Fig. 14·23, B).

(*ii*) The middle gelatinous layer which is thicker towards the apex and narrower towards the middle and lower side (Fig. 14·23, B).

(*iii*) The inner gelatinous layer is narrow and is of equal width all round (Fig. 14·23, B).

(*iv*) The prismatic layer is also of equal thickness all round.

(*v*) The innermost layer or the reticulate layer that is next to the intine or the endosporium and invests it all round except at the papilla. None of these layers cover the papilla (Fig. 14 23, B).

The intine is also distinguishable into two layers, the inner layer and the outer layer. Both of them extend over the papilla.

The nucleus is located in the apical papilla (Fig. 14·24) and is surrounded by finely granular cytoplasm. The basal region of the spore is filled with coarse granules of starch, albuminous substances and oil globules that are embedded in the cytoplasm of this part (Fig. 14·24). Machlis and Rawtisher-Kunkel (1967) described a similar structure for the Megaspore of *Marsilea vestita*. When immersed in water the megaspore exhibits a complicated structure (see Chapter VIII, Figs. 8·17 and 8·18, under the heading. "The Spores").

[illegible]

phyte. The upper smaller cell, whose exact nature is not understood, develops into the single archegonium. The prothallial cell does not divide further and serves as a nutrient cell.

[illegible] by another transverse wall [illegible] arate a **basal cell.** In some [illegible] vertical wall thus cutting off [illegible] lateral cell. [illegible] by two vertical walls in the [illegible] the first vertical wall and result in the formation of three **lateral cells** (Fig. 14 24, C), surrounding a **central cell,** which may divide by a transverse wall

orming a basal cell. The central cell surrounded by three lateral ells and a basal cell may be regarded as an archegonial initial The

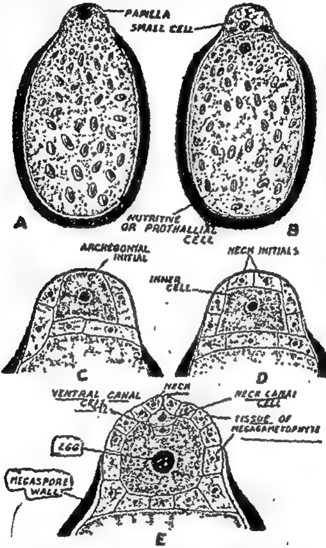


Fig. 14·24. Germination of megaspore of *Marsilea vestita.*
A. Undivided megaspore. Note that the nucleus lies in the papilla.
B. Two celled gametophyte. The first wall separates the papillate part from the lower larger prothallial cell.
C. Archegonial initial surrounded by cells of the gametophyte
D. A developing archegonium.
E. A mature archegonium. (After Compbell)

lateral cells and the basal cell divide by horizontal and vertical walls to form a tissue one layer in thickness surrounding the **archegonial initial** or the **central cell**. It divides by a periclinal wall to form an upper **primary cover cell** and a lower cell. The primary cover cell divides by two intersecting walls into 4 quadrately

arranged **neck initials** (Fig. 14·24, D). The neck initials divide by an oblique periclinal wall and form a neck of two tiers of 4 c[illegible] upper pri[illegible]al cell (Fig[illegible]unction as the **neck canal cell** of the mature **archegonium** (*M. vestita*) or it may divide to form the two neck canal cells (*M. drummondii*).

[illegible]

Fertilization. Hanstein (1865—1866) and Pfeffer (1884) described that sperms are attracted by [illegible] in the sperm lake. This is called th[illegible] The spermatozoids swarm around the [illegible]ing the megagametophyte. They penetrate the papillar envelope and reach the bell. At this stage the papillar and basal envelopes start degenerating. The spermatozoids move slowly through the bell and on reaching the more fluid sperm lake, they swim actively and reach the open archegonial necks. Only one spermatozoid enters the open neck and with its anterior end foremost penetrates the egg cytoplasm. According to Atkinson (1913) the posterior portion of the sperm touches the nuclear membrane of the egg nucleus and later it enlarges and enters the membrane thus effecting **syngamy.** Most of the sperms remain embedded in the mucilage around the egg. They straighten their coils, show senescence and die.

After, or even during fertilisation the bell, sperm lake (funnel), basal layer and inner layer coalesce into a single, homogeneous matrix with numerous sperms embedded in it.

Parthenogenetic development of the embryo has been observed by Shaw (1897) and Nathansohn (1900) in *M. macra* and by Strasburger (1907) in *M. drummondii*. Gupta (1962) states "it has been noticed in our laboratory by Senn in *M. rajasthanensis*, *M. aegyptiaca* and *M. minuta*". In such cases the unfertilised egg develops into an embryo. Strasburger (1907) reported that the megaspores of *M. drummondii* were diploid and they produced diploid megagametophytes that bear archegonia with diploid eggs. These diploid eggs develop into diploid embryo with $2n=32$.

EMBRYOGENY

After fertilisation the zygote in *M. vestita* takes 24 hours to develop into a young sporophyte bearing the first leaf. The first wall of the zygote appears within an hour. It is parallel to the long

axis of the archegonium (Fig. 14·25,

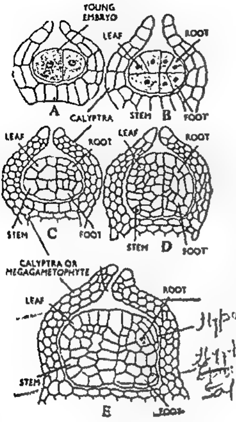


Fig. 14·25 (A—E). Stages in the development of embryo in *M. vestita*, (After Campbell).

to cytoplasmic and metabolic differences at the two poles of the zygote (Wardlaw, 1966). Leitgab (1878) stated that the plane of division of the zygote is affected by the influence of the gravity. He was able to make the zygote to divide by a first transverse wall by orienting the position of the female gametophyte so that its long axis is vertical to the force of gravity.

Hypobasal

The second wall is at right angles to the long axis of the archegonium and results in the formation of 4 cells. This is the

The octant walls are not laid ... epibasal quadrants divide by a median wall into four epibasal cells. The cells nearer the archegonial neck give rise to the *first leaf or* ... away from the ... C). The former ... as *posterior* ... quadrants are ... not median in plane but diverge strongly from the median line. The anterior hypobasal octants give rise to the *root* and the posterior to the foot (Fig. 14·25. C, D).

The primary octants giving rise to the leaf divide in a regular fashion and soon become quite distinct (Fig. 14·25, E). Further ... drical structure ... B). When all ... g the archego- ... tra (Fig. 14.25 nium divides to form ... A—E). The thickness of the calyptra at the base of the archegonium remains one layer of cells only (Fig. 14·25, A—E). The calyptra grows along with the embryo so that the latter is enclosed within

even at a stage when all the primary organs have taken shape. The first leaf or the cotyledon develops on lamina and remains cylindrical. The stem or shoot apical cell develops from one of the cells of the posterior epibasal octant (Figs. 14·25, D; 14·26, B). Adjoining cell may develop into a second leaf.

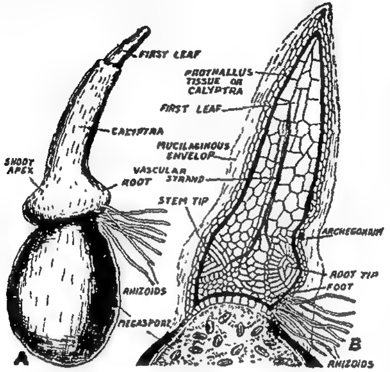


Fig. 14·26 (A—B). *Marsilea.*

A. Mature female gametophyte bearing young embryo that has pierced through the calyptra.

B. Median longitudinal section through megagametophyte and developing embryo surrounded by sheath or calyptra.

(After Sachs).

The first root develops from an apical cell distinguished in the [illegible] f this [illegible] rates [illegible] and [illegible] yptra (Fig. 14·26, A).

The foot develops from the posterior hypobasal octants. The cells divide regularly first and then irregularly to form a small foot (Fig. 14·25, E). The basal region of the young sporophyte is in direct contact with the food stored in the prothallial cell and performs the nutrient absorbing or haustorial function.

The first leaf soon pierces through the calyptra and appears as an awl-shaped or cylindrical structure without any lamina (Fig.

14·27, B). It is not circinately coiled. The first few leaves are of this type. The leaves that appear later are spathulate (Fig. 14·27,

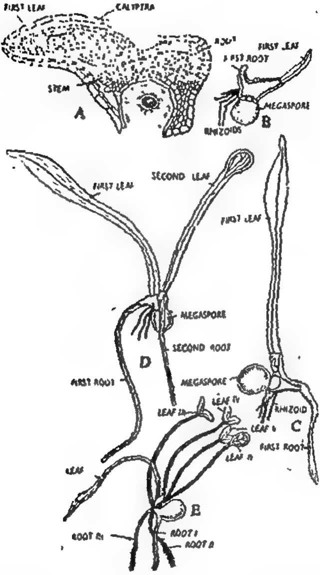


Fig. 14 27. *Marsilea.*
Later stages in the development of embryo (For explanation see text)

C—E) and then two lobed, four lobed and ultimately leaves with distinct four leaflets or pinnae appear. These are circinately coiled in young condition.

The ... bryos of *Marsilea*, ... shape of the root. ... become lobed.

The sporocarps of some species of
eir nutritious value. Bailey (1892)
, the sporocarps of *M. drummondii* yield a starch that can be made into a paste and later cooked into cakes that were eaten by the aborgines in Australia. The sporocarps of *M. salvatrix* have a great nutritious value and were a means of subsistence for the Burke expedition into the interiors of Australia.

CHAPTER XV

PTEROPHYTA—LEPTOSPORANGIOPSIDA—SALVINIALES

The order salviniales of the class *leptosporangiopsida* is a smal assemblage of aquatic and free floating ferns. The order is characterised by the following features.

1. The order includes two genera (*Azolla* and *Salvinia*) that are free floating in water. *Azolla* has unbranched and pendent roots. Roots are absent in *Salvinia*.

2. The sporangia are borne within sporocarps whose morphology is quite different from those of *Marsilea* because a sporocarp is represented by a single sorus. The indusium of the sorus is the sporocarp wall.

3. The sporangia have no annulus and develop in a basipetalnus manner.

4. The microsporangia contain numerous microspores and the megasporangia have only one megaspore each. The microspores in *Azolla* are embedded in **massulae** that are studded with anchor-shaped bodies called the **glochidia**. The massulae are formed from the tapetal plasmodium.

5. The gametophytes are much reduced.

6. The stem is horizontal and much branched with a reduced stele.

7. The leaves are not circinately coiled in the bud condition.

Christensen (1938) divided the order into two families each represented by a single genus. *Salvinia* Guettard with its 12 species belongs to the family *Salviniaceae* and *Azolla* Lamarck with 6 species is put under the family *Azollaceae*.

Family SALVINIACEAE

The family is characterised by the following features (characters of the genus *Salvinia*) :—

1. The sporophyte has a much branched, hairy and horizontal stem that floats on the surface of water.

2. The roots are absent.

3. The leaves are borne in groups of three and the groups are arranged in alternating rows. Two leaves out of a group are green, cordate, entire and floating, with papillose upper sides. The upper side also bears hair that may be stalked, branched and colourless or it may be greyish-hairy. The ventral sides of these two green leaves bear brownish hair that form a dense mat. The third leaf of the group is submerged under water and is long, filiform,

and bears numerous root like filaments (Fig. 15·1. B). These submerged or 'water leaves' act as balancers and also absorb nourishment from the water.

4. The two kinds of sporocarps (microsporangiate and megasporangiate) are borne on the 'water leaves' (Fig. 15·1, C). Both types of sporocarps may occur in groups near the bases of the leaves or may be arranged in opposite pairs all along the length of the filamentous pinnae. The smaller sori are megasporangiate and larger microsporangiate.

5. The microsporangia are long stalked and their capsules contain 64 microspores each. The megasporangia contain eight megaspore mother cells but only one megaspore survives.

6. The megaspore has a perispore external to the exine or the exosporium.

7. The microspores start germinating within the microsporangia and later come out by penetrating its wall. The microgametophyte consists of two small antheridia, the upper with 2 spermatids and the lower with four.

8. The megagametophyte bears a few archegonia with short necks.

9. The embryo produces no root.

SALVINIA GUETTARD

It is represented by about twelve species ...st of which are

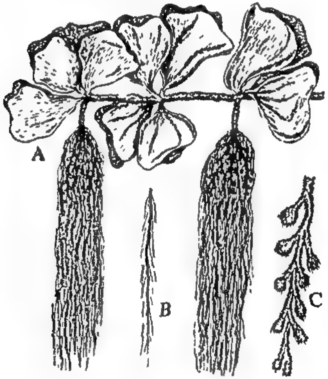


Fig. 15·1. *Salvinia auriculata* Aubl.
A. Portion of a plant showing habit.
B. Submerged leaf.
C. Submerged leaf with sporocarps.

found in the African countries. *Salvinia natans* and *S. auriculata* occurs in India. *Salvinia natans* is found in abundance in the Dal lake at Kashmere (Srinagar). It is an annual species, others are perennial.

SPOROPHYTE GENERATION

External Characters. The sporophyte (Fig. 15·1, A) has a herbaceous branched, horizontal and floating rhizome. The rhizome is beset with whorls of leaves that cover it from view. The leaves arise is clusters of three (Fig. 15·1, A) and the point from where they arise may be called the node. Two leaves of the cluster are above the surface of water and the third one is submerged. The floating and submerged leaves differ in morphology. The former being green, ovate, hemispherical, or even oblong in shape. Their upper surface is papillose and covered with stiff hair that save it from being wetted. The lower surface is brownish and also covered with hair of the same colour. These leaves may assume a boat like

are multicellular and may absorb water and other nutrients. The tips of the hair in some species have spongy tips which indicate their function as water absorbers. A bud arises at the stem node between the floating and the submerged leaves. The floating leaves are arranged in two alternate rows, the third row is of the submerged leaves. The three leaves of a node alternate with the three leaves of the next node and so on, so that there are actually *six rows of* leaves The roots are absent.

Loyal and Grewal (1967) discussed the *morphology of S. auriculata* and pointed out an interesting feature that the symmetry of the stem is bilateral in *the internodal* region and radial in the nodal region. *They are of* the opnion that the bilateral symmetry of the internodal region is derivable from the radial symmetry. The stem is beset with numerous multi cellular hair with "sharply pointed terminal cells". They regard the submerged leaf as submerged organ. Bonnet (1955) *regarded it* as an axis bearing root axes. In *S. auriculata* the *submerged* organ arises from between the main stem and the lateral branch and is disposed towards the ventral side. The floating leaves in this species are *inserted* slightly in an alternate manner and not opposite (Loyal and Grewal, 1967). One of the two leaves is smaller in size so that they are anisophyllous. The leaves are conduplicate in young *condition*. Venation is closed.

Vegetative propagation is effected by fragmentation. The fragile, rhizomes and their lateral branches easily break and the separated parts *of* the sporophyte develop into new *individuals*. Like this the plants spread rapidly under favourable conditions. *In S. auriculata* the vegetative propagation is the chief source of reproduction as its spores are *not viable*. Vegetative propagation is mainly affecte l by the lateral branches that easily separate from

main stem and grow into new plants. These lateral branches are formed from the nodes and appear in larger numbers in each plant.

Anatomy. A transverse section (Fig. 15·2, E, F) of the rhizome reveals a distinct outer layer of thin-walled cells called the

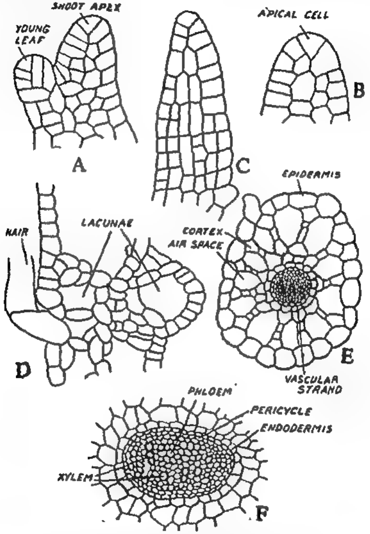


Fig. 15·2. *Salvinia natans.*
A. Stem apex as seen in horizontal section.
B. Leaf apex of a young leaf.
C. L.S. of a leaf segment of submerged leaf.
D. Section of aerial leaf showing air spaces.
E. T.S. of stem.
F. T.S. of stelar region showing details.
(After Campbell)

epidermis. It is covered with a thin cuticle and there are no stomata. Next to it is the [illegible] central stele is surrounded b[illegible] followed by a layer of thin-wall[illegible] F). The centre is occupied by parenchymatous cells with one or

more scattered
broken patches
the xylem. The [illegible]
siphonostele. In *S. auriculata* Loyal and Grewal (1967) described the stele to be an amphiphloic siphonostele in the internode and a siphonostele in the nodal region. The protoxylem is mesarch. The vessels are absent and the tracheids possess, spiral, annular, annular-spiral and scalariform thickenings. The phloem lacks companion cells and consists of sieve tubes and parenchyma cells.

The floating leaves have a lacunate mesophyll (Fig. 15·2, D) sandwiched between two epidermal layers. It is not differentiated into palisade and spongy parenchyma. Both the epidermal surfaces are covered with multicellular hair. The origin of the leaf-trace, in *S. auriculata* is extramarginal (Loyal & Grewal, 1967). The submerged leaf or submerged axis also reveals a siphonostele near its base but higher the siphonostele breaks into two independent steles and as we proceed upwards there are a large number of smaller ectophloic steles. The parent stele near the base is amphiphloic. In the segments of the submerged leaf (called root axes by Bonnet) the xylem is eccentric and consists of one or two tracheids. Two patches of phloem can be made out on either side of the xylem. A single layered pericycle and endodermis are also distinguishable.

The stem grows by means of a three sided apical cell (Fig. 15·2, A) that cut off segments from all its sides. Each segment divides periclinally into a dorsal and a ventral cell.

Reproduction

Sporocarp. The sporocarps may be borne in clusters or in

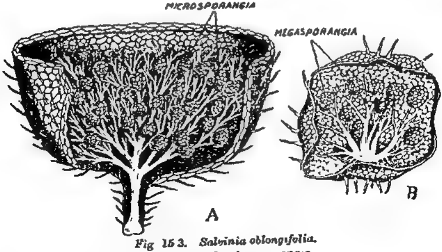


Fig 15·3. *Salvinia oblongifolia.*
A. Sporocarp with microsporangia.
B. Sporocarp with megasporangia
(After Martins from Eames, 1936)

rows on the segment of submerged leaves. Their number, in

S. natans, varies from 4—25 or even more. A sporocarp is borne at the tip of a segment. In a group, therefore, the sporocarps are sympodially arranged. The first formed sporocarps are megasporangiate (Fig. 15·3, B) and contain up to 15 or more megasporangia. The later formed sporocarps are usually micro sporangiate and are comparatively larger in size and number. They

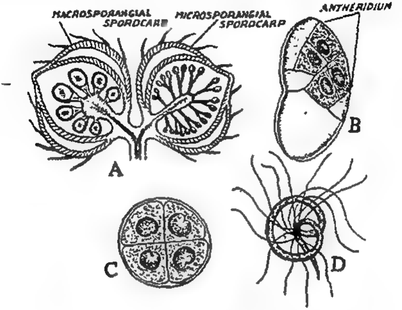


Fig. 15·4. *Salvinia natans*.

A. Sporocarps with receptacles and sporangia. The receptacle is unbranched in megasporangiate sporocarp
B. Microgametophyte with antheridium.
C. Microgametophyte as seen from above.
D. A spermatozoid.

(A, after Luerssen ; B—D, after Campbell).

contain many microsporangia that are borne on branched receptacle (Fig. 15·3, A). The sporocarps may be spherical, globose, or flattened in shape. The surface is usually smooth and covered with hair in young specimens. The flattened sporocarps of some species have ridged sides. The megasporangiate sporocarps in *S. natans* have unbranched receptacles (Fig. 15·4, A) whereas in *S. oblongifolia* the receptacle is branched (Fig. 15·3, B). The wall of the sporocarp is comparable to the indusium of the sori in *Marsilea*. It is two layered thick (Fig. 15·5, E, F). At the tips the wall layers increase in thickness and are composed of elongated and closely packed cells (Fig. 15·5 E, F). Lower down the two layers enclose small and large lacunae or air chambers. The lacunae near the base of the sporocarp are traversed with filamentous trabeculae that arises from the receptacular surface (Fig 15 5, E, F).

From the base of the sporocarp arises a thick column like receptacle that is unbranched in the megasporangiate sporocarps *S. natans* and branched in the similar sporocarps of *S. oblongifo* The receptacle in the microsporangiate sporocarps of all species

branched (Fig. 15·3, A, 15·4, A). The receptacle is traversed by the vascular strand of the leaf segment on which it is borne terminally (Fig. 15·6, E, F).

The sporocarp develops from a single apical cell (Fig. 15·5, A) that cuts of segments along its two sides. It soon forms a sorus primordium (Fig. 15 5, B). The primordium is soon surrounded by an outgrowth on all sides. This is the *indusium* (Fig. 15·5, B, C) which later covers the entire sorus. The superficial cells of *sorus* act as sporangial initials. The cells derived from the soral primordium grow to form a receptacle with sporangia arising from its distal end as well as the sides (Fig. 15·5, C—F). In the megasporangiate sporocarps only up to 25 sporangia develop whereas in the microsporangiate sporocarps the receptacle become branched and many sporangia develop (Fig. 15·3, A) in it. The development of the sporangia is strictly leptosporangiate.

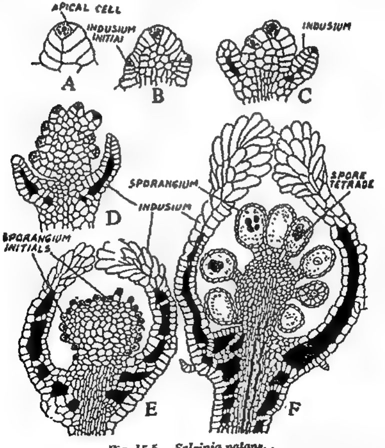


Fig. 15 5. *Salvinia natans*.
A—F. Stages in the development of sporocarp and sporangia. (After Zawidzki)

In *S. auriculata* (Loyal and Grewal, 1967) the wall of the sporocarp is three layered. The innermost layer is perforated by stomata and has cells with sinuate cell walls. Presence of small

3–5 celled hair has also been recorded on this layer (Loyal and Grewal, 1967). The stomata are restricted to the basal region. In *S. natans* they are scattered all over the surface. Air chambers are present between the inner and middle layers. Number of trabeculae arise from the inner layer and connect it with the middle layer. The outermost layers are hexagonal and bear many multicellular hair. There are no air spaces between the outer two layers.

Sporangia. The megasporangium has a short **stalk** and an ovoid or globose head or the **capsule** (Fig. 15·5, F). The capsule has a single layered wall made up of thin walled cells. Next to the wall is a single layered tapetum, which encloses eight megaspore mother cells that divide meiotically to form 32 megaspores. All the megaspores except one degenerate. The surviving or the functional megaspore enlarges in size and stores sufficient food. The cytoplasm of the aborted megaspores and the degenerated tapetal cells gathers around the functional megaspore and hardens to form a thick and vacuolate **perispore** (Fig. 15·6, A, B). The perispore is thicker towards the apex of the spore and forms a complex pollen-chamber-like structure of a gymnosperm seed (Fig. 15·6, B). The perispore at the base of this chambered region becomes slightly raised and forms a small protuberance or a mound with three lateral flaps

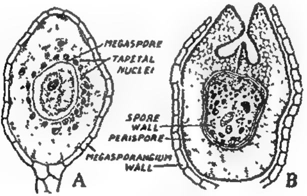


Fig. 15·6. *Salvinia natans.*
A. Megasporangium with the surviving megaspore surrounded by plasmodial mass.
B. Mature megaspore with perispore.
(A. after Kundt; B. after Arnoldi)

(Fig. 15 6, B). This mound also encloses a three sided cavity with three raised processes or ridges. The three flaps of the central mound lie exactly above the triradiate mark of the megaspore and separate during spore germination. The wall of the megaspore has the usual two layers, the exine which is surrounded by the perispore and the intine which is thin and encloses the uninucleate spore cytoplasm. The nucleus lies surrounded by granular cytoplasm at the tip of the megaspore. The rest of the megaspore is full of more fluid cytoplasm that is filled with coarse granules of stored The megasporangia have no annulus.

microspores. Both the types are endosporic and start development prior to the dehiscence of the sporangia.

Megagametophyte. The first division of the nucleus, which lies in the apical portion of the horizontally floating megaspore, leads to the formation of a small and a lenticular upper cell and a large basal cell that is filled with food material. The upper small cell divides repeatedly to form a cellular tissue of the gametophyte. It divides first by an anticlinal division to form two unequal cells (Fig. 15·8, A). Since the megaspore is swimming in a horizontal direction,

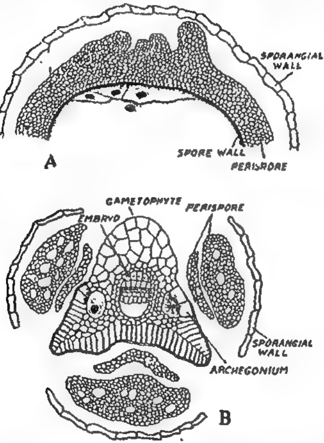


Fig. 15·8. *Salvinia natans.*

A. Median L.S. through apex of megaspore showing portion of megasporangial wall, perispore and early divisions in the apex of the megaspore.

B. Transverse section pasing through the apical region of the germinated megaspore showing the sporangaial wall, six lobes of the perispore and the gametophyte, which appears triangular in outline and has two young archegoina embedded in it. Young embryo is also seen. (After Lasser)

this division appears to form an upper and a lower cell. The upper cell is larger. Further divisions in these cells result in the formation of a thick and lobed apical cushion that breaks through the spore wall and the perispore (Fig. 15·9, A). The three lobes of the

perispore separate and diverge. The archegonia appear on this apical cushion. The first archegonium develops in the larger segment and later, two more develop on either side of the first (Fig. 15·8, B). The longer axis of the archegonia, in a floating megagametophyte, are parallel to the surface of the water. The apical cushion at this stage has protruded out of the megaspore wall and appears triangular in a cross section (Fig. 15·8, B). It has a small, upper - protuberance

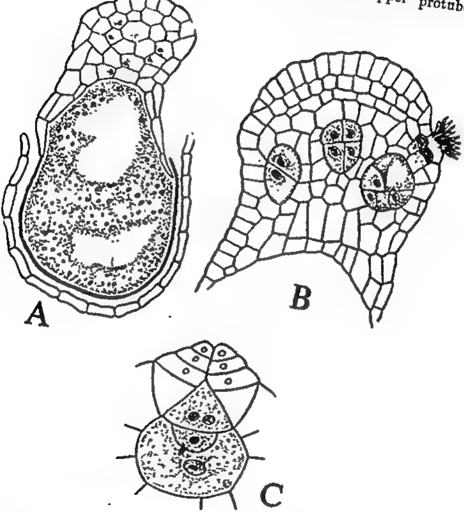


Fig. 15·9. *Salvinia natans.*
A. Showing the apical cushion and the lower multinucleate portion the female gametophyte.
B. Upper cushion with three archegonia containing young embryos.
C. A mature archegonium.
(A, B, after Arnoldi; C, after Yasui)

or a mound and a marginal meristem around the lower side. The meristem develops into two wings that extend background over the sides of the megaspore wall and serve as balancing organs for the floating megagametophyte.

Meanwhile the nucleus of the lower larger cell below the apical cushion has undergone free nuclear division. There is no wall formation and the nuclei lie scattered in the cytoplasm (Fig. 15·9, A) of this cell. This multinucleate cell acts as reservoir of food.

The tissue of the apical cushion just around the archegonia divides in such a manner so as to orientate the archegonia through an angle of 90°. The necks of the archegonia now point upwards. The cushion may develop further and enlarge in size and grow bigger than the megaspore. Its cells turn green and if fertilisation fails to take place, more archegonia develop along the sides of the first three.

A mature archegonium (Fig. 15·9, C) has a neck made up of three tiers of 4 cells each or of 4 longitudinal rows, each row three cells in height. The neck encloses a neck canal occupied by a single, binucleate neck canal [illegible] ns an upper smaller ventral canal [illegible] prominent female nucleus (Fig. 1[illegible] rchegonium is similar to that of *Marsilea*.

The portion of the female gametophyte below the apical cushion is covered by the spore wall and remains of sporangial wall (Fig 15·9, A).

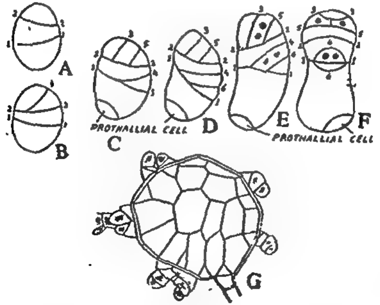


Fig. 15·10. *Salvinia natans.*
A—F. Stages in the development of male gametophyte.
G. Dehiscence of sporangium and escaping male gametophytes.
(A—E, after Belajeff, G, after Pringsheim).

Microgametophyte. The microspores complete their germination within the microsporangium. They remain embedded in the

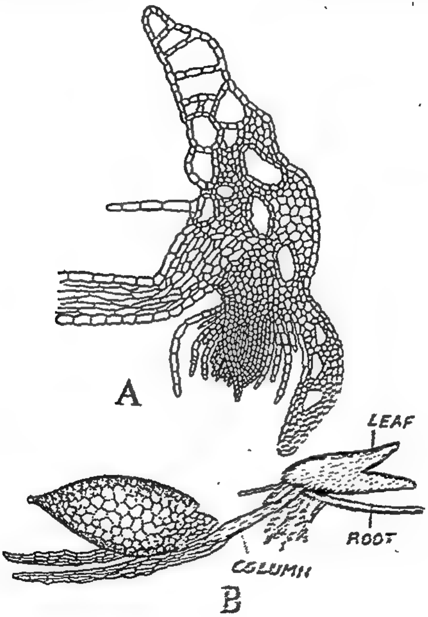
massulae during their course of development. The contents of the microspore divide into three cells by two transverse (Fig. 15·10, A, 1—1, 2—2) divisions. The lowest cell of the row divides by another transverse or oblique transverse wall (Fig. 15·10, C) to form a small lenticular **male prothallial cell.** Further divisions take place only in the two upper cells (Fig. 15·10, C—E), which act as antheridial initials; the lower cell and the prothallial cell remain undivided. Each antheridial initial divides by a diagonal wall (Fig. 15·10, B—C, 3—4) that intersect the walls 1—1 and 2—2. This results in the formation of a peripheral smaller jacket cell and a large **sister cell** in the upper antheridium. The lower antheridium has a peripheral cell parallel to the wall 2—2 and large triangular sister cell (Fig. 15·10, C). The sister cells in both the antheridia divide dy walls 5 and 6 which again intersect (15.10, D) the walls 2—2 and 1—1 respectively, thus forming two sterile jacket cells and a spermatogenous cell in each antheridium. The **spermatogenous cell** of each antheridium forms a group of 4 **spermatocytes.** The spermatocytes are not surrounded by jacket cells on all sides, but are in contact with the spore wall on one side (Fig. 15 10, D). The undivided basal cell elongates considerably (Fig. 15.10, E) and pushes the upper two antheridial cells out of the massula and the microsporangial wall. The jacket cells disintegrate and the spermatids containing multiflagellate spermatozoids are liberated by the decay of the spore wall.

Fertilisation. The neck canal cell and the ventral cell disorganise and the neck cells spread apart to create a passage for the spermatozoids to enter and effect fertilisation. Large number of sperms gather around the open necks, but only one is able to penetrate the egg and effect fertilisation.

EMBRYOGENY

The first division of the zygote is parallel to the long axis of the archegonium and forms two unequal cells (Fig. 15·9, B). The second wall is transverse (at right angles to the long axis of archegonium) and forms a quadrant (Fig. 15·9, B). Each cell of the quadrant divides dy vertical walls to form an octant stage. The hypobasal octants develop into the foot which is haustorial in nature. The two anterior epibasal octants develop into the first leaf. Out of the two posterior epibasal octants one gives rise to the stem apex, whereas the other is functionless. There is no root in *Salvinia*. The upper and the lower octants divide by periclinal walls to form a central plate of eight cells. The cells of this plate divide repeatedly to form a column like structure in the centre. It connects the foot with the leaf and the stem apex (Fig. 15·11, A). Growth of this central column pushes the leaf and the stems out of the gametophytic tissue (Fig. 15·11, B). Some workers interpret that there is an embryonic root that does not grow further and mixes with the foot. They call such a root as **vestigial root** Others interpret that the column and the foot both represent a single enlarged foot of the embryo. The leaf segment grows into a cordate or a sagittate leaf raised on the column. The stem apex is present below the leaf and faces the gametophyte (Fig. 15·11, A). The column is traversed by

a central vascular strand that extends from the foot to the leaf base, where it bifurcates and sends one branch to the leaf and the other to the stem apex. The stem apex divides actively and forms the rhizome which bears two floating leaves. Later the rhizome bears



Family AZOLLACEAE

The family is characterised by the following features (Characters of the only genus *Azolla* Lamarck) :—

1. The sporophyte has a horizontal and branched stem, bearing leaves and roots.

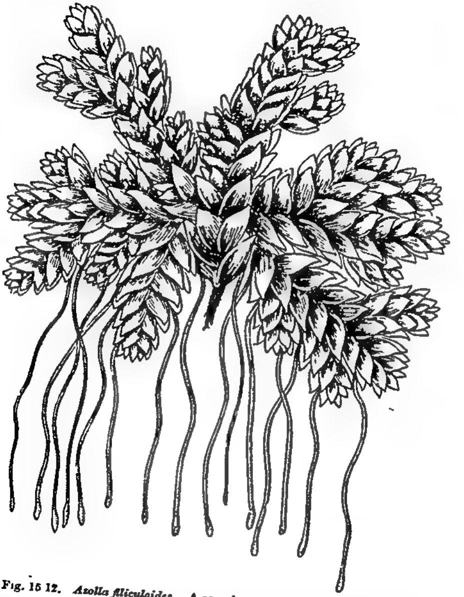


Fig. 15 12. *Azolla filiculoides*. A complete plant showing habit.

2. The leaves are borne in two alternating rows and are small in size. Each leaf is divided into two lobes. The upper lobe is green in colour (later becoming red), has stomata and lacunae filled with filaments of *Anabaena azollae*. The lower lobe is submerged under water and is thin.

3. The roots are unbranched.

4. The stem [redacted] traversed by a medullated protostele (siphonostele).

5. The sporocarps are borne on the lower and submerged lobes of the eaves and are of two kinds. The larger ones are megasporangiate and contain numerous microsporangia. The smaller ones are microsporangiate and contain a single megasporangium. Sometimes bisporangiate sporocarps are also found.

6. The megasporangia and the microsporangia contain abundant, mucilaginous plasmodial fluid that differentiates into massulae. The megasporangium has 4 massulae, one of them has the single megaspore embedded in it. The microsporangium has many massulae studded with glochidia. The microspores are embedded in these massulae. The glochidia become entangled with the massulae bearing megaspores. Both sink to the bottom where the gametophytes develop and fertilisation is effected.

7. The male gametophyte contains only one antheridium which produces eight spermatozoids.

8. The megagametophytes bears one or several archegonia.

9 The embryology [redacted] similar to other leptosporangiate ferns. The young sporophyte with one leaf rises to the surface of water carrying the massulae along with it.

Azolla is represented by thirty one species out of which six are extant species. *Azolla filiculoides* is found in India, Britain and North America. Taxonomically the species of *Azolla* are placed in four sections of the genas. Only two out of these are well known (*Rhizosperma* and *Azolla*). These sections are based on the characters of massulae and megaspore apparatus as follows :—

1. Section *Azolla* : . Massulae have hooked on anchor-shaped glochidia. Megaspore apparatus has three floats in the swimming. apparatus.

It is represented by many species, *i.e*, *A. filiculoides*; *A. microphylla*, *A. mexicana*, etc.

2. Section *Rhizosperma* : Massulae either with straight, simple or branched glochidia or without them. Megaspore apparatus has [redacted] floats, *e.g.*, *A. prisca*, *A. turgica*, *A. nana*, etc.

3 Section *Antiqua*. Glochidia not known. Megaspore has [redacted] floats of equal size. Represented by one fossil species.

4. Section *Filifera*. Glochidia hair like, coiled or knobbed. Megaspores not known. Represented by one fossil species only.

AZOLLA Lamarck

In India, the genus is represented by *Azolla filiculoides* Lam., which is widely distributed and occurs free floating on the surface of water in road side ponds, pools, reservoirs and lakes. It prefers undistributed and standing waters. The plants resemble small and delicate moss gametophyte and cover the entire surface of water. Young plants have green or bluish green leaves which turn red at maturity so that they can be recognised from a distance.

SPOROPHYTE GENERATION

External Characters. The sporophytes (Fig. 15·12) are small in size and are distinguished into stem, leaves and roots. The stem

is horizontal and profusely branched. It is thickly covered with leaves that overlap each other and are arranged in an alternate manner. The roots arise from the under side of the stem and are unbranched The leaves are small in size and are divided into two lobes that are usually of equal size. The dorsal lobe is aerial and green. It is thick and sterile. The ventral lobe is thin, almost colourless and submerged in water. The bilobed leaves arise from the dorsal surface of the stem and are arranged in two alternate rows. The dorsal or the upper lobe has its dorsal side facing towards the sky. It encloses large mucilage filled cavities that harbour filaments of *Anabaena azollae* Strasb., that lives as long as the leaf containing it. Oes (1913) observed that there is a symbiotic relationship between the alga and the plant. The alga fixes free nitrogen of the air for the plant and latter gives it shelter and food. The same

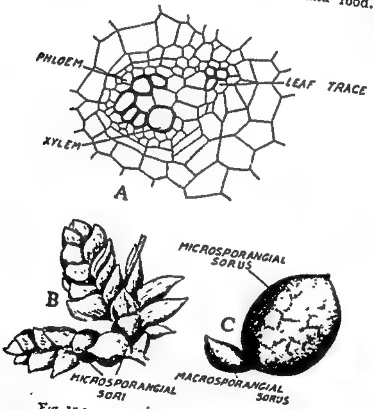


Fig. 15 12 (A—C). *Azolla filiculoides.*
A. T.S. part of stem showing stele and a few layers of cortex.
B. Portion of a plant bearing microsporocarps.
C. Mega-and Micro-sporocarps.

(A, after Quera; B—C, after Cambell)

species of *Anabaena* occurs in the leaves of *Azolla* all over the world, which indicates that dispersal by means of vegetative parts plays a greater role than the spores. The younger portion of the stem is upwardly curved. The leaves are not circinately coiled in the bud

condition. The submerged lobe of the leaf is believed to absorb water. It is mostly one layer of cells in thickness except the basal part which is thicker and encloses a row of air chambers.

Vegetative propagation is effected by means of fragmentation of the stem and separation of the lateral branches. This rapid method of multiplication leads to enormous increase in the number of plants. **Azolla filiculoides** is annual The closely packed leaves enclose small spaces between them. They are filled with air and are one of the means to keep up the buoyancy of the plant. Small papillae can also be seen on the upper surfaces of the aerial lobes.

Anatomy. The stem of *Azolla* like that of *Salvinia* grows by means of a three sided apical cell that cuts off segments from all the three sides. A transverse section of the mature stem (Fig. 15·13, A) reveals a distinct epidermis followed by a parenchymatous cortex that is 4 to 8 cells in thickness. Unlike *Salvinia* there are no lacunae or air spaces in the cortex. The innermost layer of cortical cells, endodermis and pericycle are derived from a common mother cell layer. The endodermis is not very distinct and is single layered (Fig. 15·13, A). The pericycle is also one layered and completely encircles the vascular elements. The vascular cylinder consists of a few xylem tracheids (Fig. 15·13, A) and phleom elements that are twice the number of xylem elements. It is not possible to determine the stelar type (Fig. 15·13, A) as there is a great reduction in the vasculature of the stem in response to aquatic mode of life. Smith (1955) regards it to be protostelic, whereas Eames (1936) describes it to be 'apparently siphonostelic'. Leaf and branch traces also arise from the central cylinder and most probably leave gaps. Eames (1936) described that "the leaf trace forks dichotomously before [illegible] T[illegible] iphonostelic with 5—10 [illegible] rds the outer border [illegible]

The dorsal lobe of the leaf reveals the two epidermal (Fig. 15·14, A) layers with stomata on both of them. The upper epidermis is beset with numerous one or two celled hair. In a young leaf the [illegible] ear its base. The cavity opens to the [illegible] The [illegible] [illegible] closes by the development [illegible] the pore thus imprisoning [illegible] A) The pores become fill[illegible] [illegible]age. [illegible]ere is a well defined palisade tissue that fills the whole leaf and encloses small and large air spaces (Fig. 15·14, A).

The roots are adventitious and arise endogenously from a single mother cell that gives rise to the inner cortical layer, endodermis and pericycle of the stem. This cell divides by a few oblique walls to cut off a tetrahedral apical cell of the root, with four cutting faces (three lateral and one outer). Transverse section of mature root (Fig. 15·14, C) reveals the following structure:

There is a single layered epidermis that is composed of thin walled parenchymatous cells. It encloses two layers of parenchymatous cortex. The outer layer of cortical cells consists of 9 cells whereas the inner layer is composed of six cells (Fig. 15·14, C). The endodermis is also composed of 6 cells that appear rectangular in a transverse section (Fig 15·14, C). The pericycle is also composed of

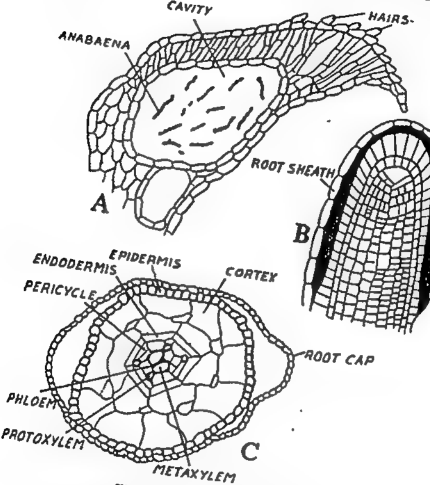


Fig. 15·14. *Azolla filiculoides.*
A. Dorsal lobe of leaf as seen in a longitudinal section.
B. L.S root apex showing root sheath, apical cell and other embryonic tissues.
C. T.S. root.

(After Campbell)

six cells The stele consists of four protoxylem and two metaxylem tracheids (Fig 15·14, C). Phloem is represented by 4 sieve tube cells. The mature roots bear root hair, a little behind the root tip. The epidermal cell giving rise to root hair divides into two cells by a diagonal wall. One of these cells grows into a unicellular root hair whereas the other functions as the epidermal cell. Leavit (1902)

observed that the apical cells of the roots that cease to grow in length may divide into a number of root hair cells that elongate and grow into a cluster of root hair.

Reproduction. The sporocarps are borne on fertile leaves. The oldest leaf (first formed or lowermost) of a lateral branch is always fertile. According to Eames the submerged lobe (ventral lobe) of this leaf becomes bilobed or nearly four lobed and each lobe

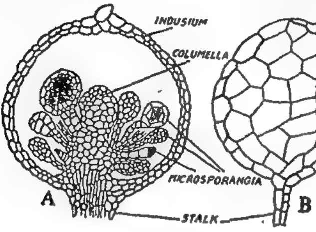


Fig 15·16 (A—B). *Azolla filiculoides.*
A. Microsporangiate sporocarp in section B. A microsporangium. (After Campbell)

is terminated by a sporocarp. A marginal and laminate outgrowth from the dorsal lobe of the fertile leaf forms a hood-like structure that covers the sporocarps According to Strasburger (1873) the sporocarps arise in the axil of the dorsal lobe of the fertile leaf. The sporocarps are of two types : (*i*) the smaller macrosporangiate or megasporangiate sporocarps that contain only one megasporium, and (*ii*) the large or microsporangiate sporocarps that contain numero'us microsporangia The megsporangiate sporocarps are more or less oval or ellipsoidal in shape whereas the microsporangiate sporocarps are spherical. The megasporangiate sporocarps (Fig. 15·17, E, F) bear a single megasporangium at its base on a small receptacular surface. It is covered by an indusium or sporocarp wall. The indusium is two layered. It is composed of thin walled cells which become thick walled and hard at the apex of the

sporocarps (Fig. 15·16) bears long, unbranched stalks arising

even elongated **receptacle** or **columella** (Fig. 15·15, A).

The development (Fig. 15·17, A—F) of the sporocarp follows a very simple course. The young megasporangiate sporocarps

tial has cut

the

This is the prim... ...arp wall. This ring of c... ...and surrounds it on a... ...cells of the indu- sium ... and make it two-layered thick. A few

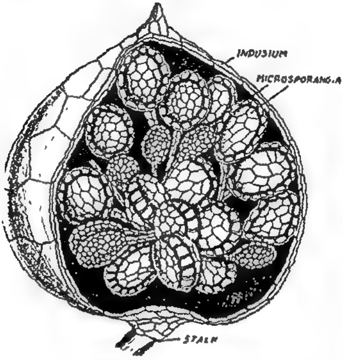


Fig 15 16. A microsporangiate sporocarp of *Azolla filiculoides*. One side is removed.

segments or hormogonia of *Anabaena azollae* are also present within the indusium (Fig. 15-17, B). The free margins of the indusium, at the top, grow towards each other and close the opening (Fig. 15-17, C, D). The megasporangial initial develops in a leptosporangiate manner into a mature megasporangium which has a single layered wall, a single layered tapetum that encloses eight megaspore mother cells. The stalk of the megasporangium divides repeatedly to form a thick and columnar structure (Fig. 15-17, C, D). Some superficial cells of the sporangial stalk function as sporangial initails which remain dormant. This reveals the receptacular nature of the stalk. The eight mother cells divide meiotically to form 32 spores out of which only one matures (Fig. 15-17, E, F). This is the functional magaspore. Others 31 disorganise or abort. The tapetal cells have by now degenerated to form the periplasmodial fluid, which becomes organised into four massulae. One of these massulae has the megaspore embedded in it. The other three contain aborted or nonfunctional spores. The macrosporangial wall and the indusium (sporocarp wall) dehisce along a transverse line (Fig. 15-18, A). The apical portion of the ruptured megasporangial wall and the indusium and the three massulae containing the non-fuctional megaspores remain in contact

with the fourth massula containing the functional megaspore (Fig. 15·18, B). The lower portion of the ruptured sporangial wall and the indusium separate from the massulae and the upper part. The

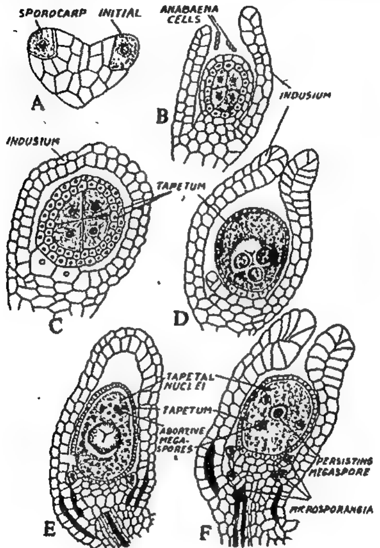


Fig. 15·17 (A—F). *Azolla*. Stages in the development of sporocarp and megasporangium.
A—E. *A. filiculoides*. F. *A. caroliniana* (F, after Pfeiffer)

upper portion containing the massulae and the cap like upper indusial and sporangial [illegible] apparatus" [illegible] swimming. [illegible] megaspore and the massulae along with the attached sporangial and indusial wall sink to the bottom.

In case the megasporangium fails to produce a functional megaspore the sporangial initials developed on its stalk undergo further

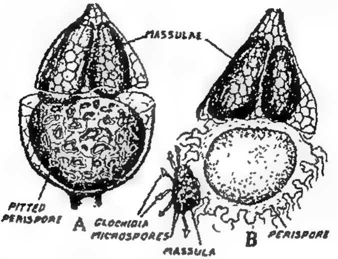


Fig. 15·18. *Azolla filiculoides.*

A. Dehisced megasporangium with four massulae (only three visible), one containing the megaspore.

B. The lower portion of the sporangial wall has been discarded. The functional megaspore with its massula is attached to the other massulae. Also note the massula with microspore and glochidia attached to it. (After Beranrd)

development and produce numerous microsporangia that have narrow, long and unbranched stalks This results in the development of a

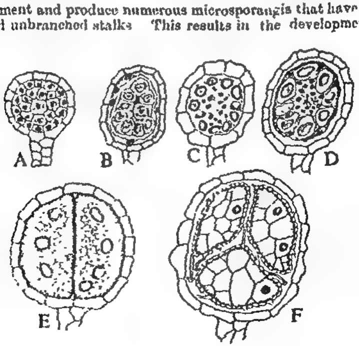


Fig. 15·19 *Azolla filiculoides.* Stages in the development of megasporangium. (After Hannig)

larger microsporangiate sporocarp. The development (Fig. 15·19, A—F) of the microsporangium is similar to that of the megasporangium up to the formation of 8 spore mother cells. In the microsporangium all the 32 microspores remain functional (Fig. 15·19). The tapetum breaks down to form the plasmodial fluid. The microspores move to the periphery of the plasmodial fluid (Fig. 15·19,

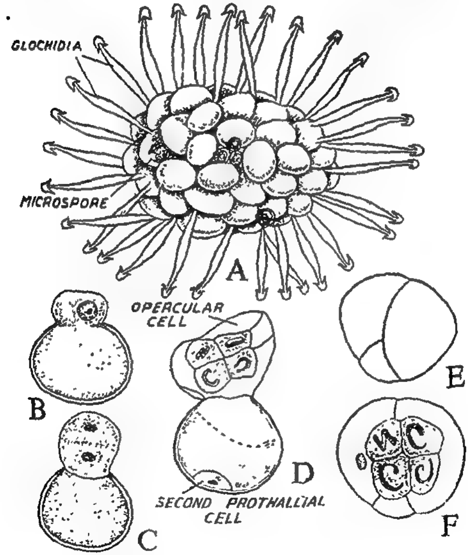


Fig. 15·20 (A—F). *Azolla filiculoides.*
A. A massula containing microspores and studded with glochidia.
B—F. Stages in the development of male gametophyte.
(After Smith)

D). The plasmodium now becomes organised into 4 or more massulae, each containing more than one microspores embedded in it (Fig. 15·19, F). The cytoplasm of the massula is alveolar. In *Azolla filiculoides* and *A. caroliniana* numerous hooked processes arise from the surface

of each massula. These are called the *glochidia* (Fig. 15·20, A). Glochidia are absent in some other species. As soon as the microspores mature the sporangial walls dehisce and the massulae containing microspores lie free in the cavity of the sporocarp. Later the indusium (sporocarp wall) also ruptures and the massulae float away under water. The massulae studded with glochidia attach themselves with macrosporal massulae (Fig 15·18, B). This attachment is effected by means of glochidia. The microsporocarps sink to the bottom before dehiscence. The massulae are liberated at the bottom and swim under water.

GAMETOPHYTE GENERATION

Microgametophyte. The microspore starts germinating within the massula in which it is embedded. Before germination the exine of microspore ruptures and the uninucleate spore contents surrounded by intine protrude out (Fig. 15·20, B). The nucleus divides into two daughter nuclei (Fig 15·20, C) one of which remains in the protuberant part and the other migrates into the spore cavity. The protuberance is then cut off from the lower vegetative cell by a transverse wall and is called the antheridial initial. The lower or larger vegetative cell then cuts off a small lenticular prothallial cell (Belajeff, 1898; Campbell, 1893). There is no further division in this cell (Fig. 15·20, D). The antheridial initial divides into three cells by oblique transverse walls (Fig. 15·20, E). Out of these three cells the distal, smaller and the basal cells do not divide further and act as the **cap cell** and the **basal cell** of the antheridium, respectively. The middle divides by two periclinal walls forming two jacket cells enclosing a central cell. One of the jacket cells divides again so that there are five jacket cells surrounding a single central or **primary androgonial cell.** It divides into eight **spermatocytes** (Fig. 15·20, D) whose protoplasts metamorphose into same number of multiflagellate spermatozoids (Fig 15·20, F). The massulae absorb water, soften and decay, thus liberating the spermatozoids into the surrounding water. This whole process is complete within seven days.

Megagametophyte. The germination of the megaspore is endosporic and is completed within 7 or 8 days. The megaspore germinates within its massula which in turn is attached to the other three massulae and the upper half of the sporangial wall (Fig. 15·18, A, B) and the indusium (swimming apparatus). The nucleus of the megaspore enlarges in size and divides into two. A cell wall is laid down between the two daughter nuclei, cutting off a small, lenticular apical cell and large basal cell which is filled with starch grains. The basal cell nucleus undergoes free nuclear division thus making it multinucleate. There is no wall formation. The upper smaller cell divides again by a vertical or a horizontal wall. Later divisions lead to the formation of a two layered apical disc of cells. At this stage a superficial cell in the middle of the upper layer acts as an archegonial initial. The megaspore wall now ruptures above the apical cushion of cells so that the latter is exposed. By further divisions, this exposed two layered discoid mass of cells develops into

a prominent protuberance composed of 5—8 layers of cells (Fig. 15·21, A). A superficial cell acts as the archegonial initial which develops into a mature archegonium in manner like that of *Salvinia*. The archegonial initial divides by a periclinal wall into an upper **cover cell** and a lower central cell. The cover cell divides into four quadrately arranged **neck cells** (Fig. 15·21, B), by two intersecting walls. The neck cells divide by transverse walls to form three or four tiers of 4 cells each (Fig. 15·21, B, D). These constitute an archegonial neck consisting of 4 longitudinal rows of cells, each row 4 cells high. The central cell divides into an upper **primary neck cell** and a lower **primary ventral cell** (Fig. 15.21, B). The former grows between neck tiers and forms a single, uninucleate neck canal cell or divides to form two neck canal cells. The primary ventral cell divides into (Fig. 15·21, D), an upper small, ventral cell and a lower large egg cell (Campbell, 1893). Smith (1955) reported that the primary ventrla cell may function directly as an egg cell. The mature archegonium opens in the usual manner forming an open neck for the spermatozoids to swim down to the egg.

In case the first archegonium is fertilised, no more archegonia develop. In case of failure of fertilization more archegonia can develop.

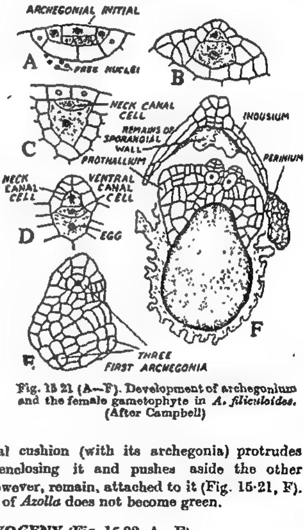


Fig. 15·21 (A—F). Development of archegonium and the female gametophyte in *A. filiculoides*. (After Campbell)

The growing apical cushion (with its archegonia) protrudes out of the massula enclosing it and pushes aside the other three massulae which, however, remain, attached to it (Fig. 15·21, F). The female gametophyte of *Azolla* does not become green.

EMBRYOGENY (Fig. 15·22, A—E)

The zygote or the oospore increases in size and divides by a transverse or an oblique longitudinal wall (Fig. 15·22, A 1—1) into two nearly equal cells. The second wall (Fig. 15·22, B) is either vertical or transverse, depending upon the plane of the first division

and forms a four celled embryo (quadrant stage). The four primary organs of the mature embryo or young sporophyte can be traced back to each cell of the quadrant stage. The two epibasal cells (nearer to archegonial neck) give rise to the first leaf and the stem, whereas the two hypobasal cells give rise to foot and the first root

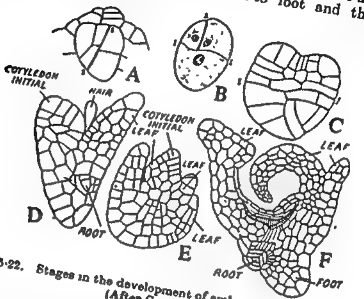


Fig. 15·22. Stages in the development of embryo in *A. filiculoides*. (After Campbell)

(Fig. 15·22, C). Except the foot the other three organs grow by means of an apical cell. The quadrants divide further to form an octant stage. The apical cells of the primary organs differentiate from their respective quadrants at a thirty-two celled stage (Fig. 15·22, C). The first leaf and the stem develop almost at the same rate. The root develops slow. The foot develops into a small cylindrical organ (Fig. 15.22, F). The first leaf overarches the stem and soon grows into a visible segment on one side (Fig. 15·22, D) The growing embryo throws off the so-called "swimming apparatus" and the embryo rises to the surface of water along with the megagametophyte, after the development of air cavities in the first leaf. The procambial strands develop into the first vascular strand that bifurcates below the stem apex giving a branch to the stem and the first leaf. It is continuous below into the first root (Fig. 15 22, F).

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